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GROWTH AND PERMEABILITY OF CENTURY-OLD CELLS

DR. D. T. MACDOUGAL

DESERT LABORATORY, TUCSON, ARIZONA

THE present paper includes an account of some of the properties of cells of the sahuaro or tree-cactus (*Carnegiea gigantea*), which show individual activity for periods of a century and even longer. Some of the noteworthy reactions of cell-masses of cacti have been brought out in previous contributions dealing with permeability and growth. Stems and fragments of plants have been found to be capable of extended existence when cut off from external supplies of water, sections have been kept alive for weeks as slide cultures, and young joints of Opuntia have been found to be capable of growth at 58° C and to sustain even higher temperatures (62° C) without injury.[1] This capacity for endurance of high temperatures has been attributed to the high proportion of pentosans in the protoplastic mass, their presence having the effect of raising the point at which included proteins might be coagulated.

Definite information of the age limit of cells in plants is scanty. It may be assumed, however, that the statement that the rays or vertical plates of parenchymatous cells which run from the pith or medulla of stems of higher plants toward the surface and are continuously

[1]MacDougal, D. T., and Earl B. Working, "Another High Temperature Record for Growth and Endurance," *Science*, *54*, 152, 1921.

elongated radially while dying away in the oldest part include cells several years old. It is highly probable that the rays of the great sequoias of California may furnish examples of ray cells which live many years, while the tree may attain an age of over thirty centuries.

The simple parenchymatous cells furnish the greater number of active long-lived cells in the higher plants. It may be safely taken for granted that any great degree of specialization will be accompanied by or result in a limitation of the period of activity. It is to be recalled that resting embryos in seeds and spores in the implied dormant condition may be alive after periods of hundreds of years, especially when protected from the action of certain environmental agencies. So far as information is available to the author the protoplasts or cells hitherto known to attain the greatest age in a living or functioning condition are those of the central nervous tracts of animals. If the current conclusion be accepted that brain cells once formed maintain a continuous and individual existence until death then it may be said that in man living cells are formed which may function for a century or a few years more. Inferentially similar cells in the larger animals may continue activity for two or as much as three centuries. In this case extended activity occurs in highly differentiated protoplasts. It has been suggested the cells of the heart likewise have an extended existence.

The two main phases of growth and hydration in plant cells have recently been described in this journal.[2] In the first stage of a cell derived from a cambium layer in a plant stem, for example, proteins and carbohydrates are synthesized and lipins or phosphatides are accumulated, the implied condensations being accompanied by the liberation of water which may be yielded to older contiguous cells. The actual dry weight of the protoplast increases during this period, and the Ph is generally on

[2] MacDougal, D. T., "Accretion and Distention in Plant Cells," Amer. Nat. *59*, 336–345, 1925.

Mature sahuaro (*Carnegiea gigantea*) near Desert Laboratory, and several young plants 3 to 5 years old: also basal part of trunk in the center of which are medullary cells over 100 years old. Living tracts of green epidermic with active (?) stomata are to be seen, which are also of great age.

the alkaline side of neutrality. In the second stage of development the cell distends, vacuolization is marked, and thickening of the wall takes place so that the dry weight of the tissue may increase while that of the protoplast may actually lessen. During this period the Ph slowly swings to the opposite side of neutrality reaching Ph 3 in some plants and even higher in fruits.

During the course of some studies on these phases of growth it was found that the medulla of the tree cactus of Arizona (*Carnegiea gigantea*) furnished material of exceptional value. The medulla is composed primarily of simple parenchymatous cells in which some tracheids are formed in advanced stages, constituting an irregular cylinder 5 to 18 cm in diameter which extends from near the base of the tree to its summit, which may be 11 to 12 m from the base. Medullary cells formed during the first five or ten years of the life of the plant remain in place and are found to be alive and functional in trees estimated to be 150 years old. As a measure of safety these cells will be designated as "century-old" cells in the present paper. (Fig. 1.)

Another feature of only indirect interest in the present connection is the fact that some of the original green epidermis formed on the plant during its first half meter of growth is retained and that the stomata retain their shape and to some extent the mobility of their guard cells. These and the living epidermal cells as well as some of the underlying cortical cells must be taken to share in the longevity of the medulla and offer many opportunities for the study of senescence. Medullary tracts of other columnar cacti may be expected to furnish living cells of great age.

The above general facts were first recognized in 1925 and a series of observations were arranged to determine the more obvious features of growth, hydration and permeability. Attention was confined chiefly to the close of the accretion period of the newly formed cells near the summit of the trunk and to the succeeding period of dis-

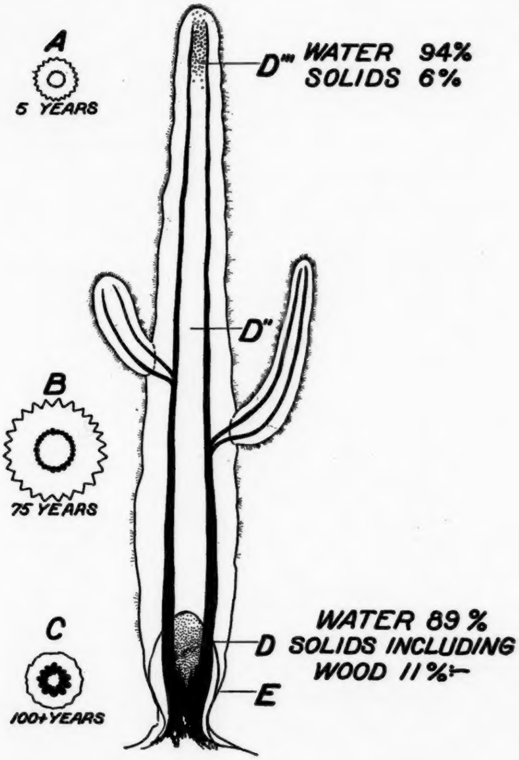


FIG. 1. Diagrams of structure of sahuaro (*Carnegiea gigantea*). A full length scheme of structure of the tree is shown, with cross sections of base *C*, median *B*, and apical *A* regions. The medulla, *D*, *D″* and *D‴*, is surrounded by an incomplete woody cylinder enclosed in a very thick succulent cortex. The age of the medullary cells in these regions is indicated as well as the water and solids in the apical and basal regions. The outline of the young plant at the base shows medullary region, active during the life of the tree.

tention. Some features of extraordinary interest were encountered.

General Anatomical Features of the Medulla

The activity of the growing point is included within a hundred days of the summer season, beginning in April

and May, and the ultimate derivatives which form the 10 cm length of medulla which constitutes the approximate average extension for the season is composed of loosely arranged parenchymatous cells with ample intercellular spaces and with contacts lightly made. It is probable that each cell makes twelve contacts originally and that this number might be increased to fourteen with the final compression in which the woody cylinder participates.[3]

The detailed history of these medullary cells is to form the subject of further studies under the direction of Professor J. B. Overton, to whom I am indebted for many illuminating suggestions, but it may be said in connection with the present paper that division of the medullary cells takes place but rarely if at all after the first season of growth, except in connection with the formation of vascular bundles. The entire mass of the medulla seems to retain its meristematic character to the end, but the secondary stage of activity includes chiefly the formation of conducting tissue which penetrate the medulla in a maze of anastomozing strands joined to the main bundles of the enclosing woody cylinder. Briefly stated, most of the medullary cells formed during the first few years continue their individual existence and activity during the entire lifetime of the tree, which may be as long as a century and a half. These estimates of the age of trees are based upon photographic records of trees of various ages for the twenty-three years since the establishment of the Desert Laboratory.

The cells of the terminal part of the medulla have an average diameter of about 245–250 microns when examined in February and March following the season of their formation. Actual growth takes place within a period of about 150 days beginning in April in the region of the Desert Laboratory. The walls in this stage present no unusual features, the plasmatic layers and

[3] See Lewis, F. T., "The Typical Shape of Polyhedral Cells in Vegetable Parenchyma and the Restoration of that Shape following Cell-division." Proc. Acad. of Arts and Sciences, *58*, 537–552, 1923.

strands and the vacuoles are of the usual type, but contain much mucilage. Droplets of fatty substances are abundant during the period of lowest temperatures, but these gradually disappear with the advance of the season, and starch accumulates. A densely packed layer surrounds the nucleus. (Fig. 2.)

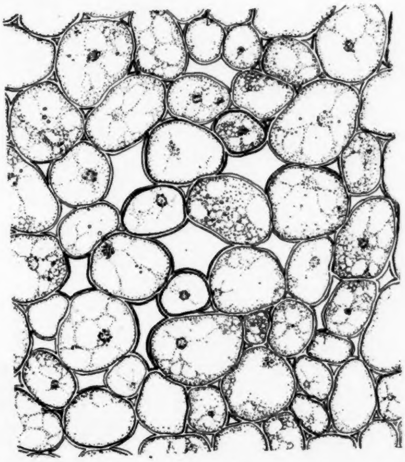


FIG. 2. Medullary cells two years old in cross section, 249 × 226 microns.

It is notable that during the next fifty years the average maximum diameter increased only to 272 microns longitudinally and 256 transversely in which the rate of distention was very slow, but was greatest in the longitudinal axis of the tree. Crystals were more numerous in the cells, the nucleus has not changed in size and a slight increase in thickness of wall was apparent. (Fig. 3.)

Distention during the following fifty to eighty years is greatest in planes radial to the axis of the tree so that the diameter in this plane reached an average of 400 microns, while in the longitudinal axis it was but 322 microns, the increase being three times as great in the radial direction as in the longitudinal. This inequality may be attributed in part to compression set up by the shrinkage in the surrounding woody cylinder. The walls

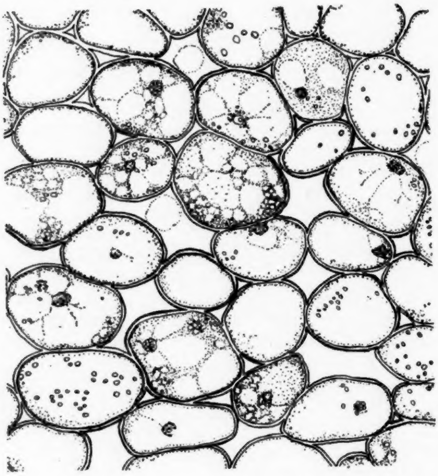


FIG. 3. Medullary cells fifty to sixty years old in cross section, 255 × 226 microns.

are measurably thicker, but the plasmatic layers are intact, while the nucleus is apparently unchanged. Mucilages have disappeared and the plasmatic mass is now noticeably granular with small bodies taken to be proteinaceous. Clumps of crystals of silica are very abundant. It is to be recalled that even in this stage the meristematic condition continues, as most of these cells would in time be transformed into vascular tissues. (Fig. 4.) In this brief description other details more pertinent to a detailed cytological study have been omitted, and attention has been confined to the features of prime interest with respect to permeability.

VARIATIONS IN CONCENTRATION OF SAP, DRY WEIGHT, ACIDITY AND H-ION CONCENTRATION

A mass of cells taken within a few cm of the apex of the stem includes very little woody tissue and such material was found to show a content of 94.3 per cent. water and 5.7 per cent. dried material. A similar mass of cells taken from the basal part of the medulla a century old in addition to the enlarged parenchymatous cells includes

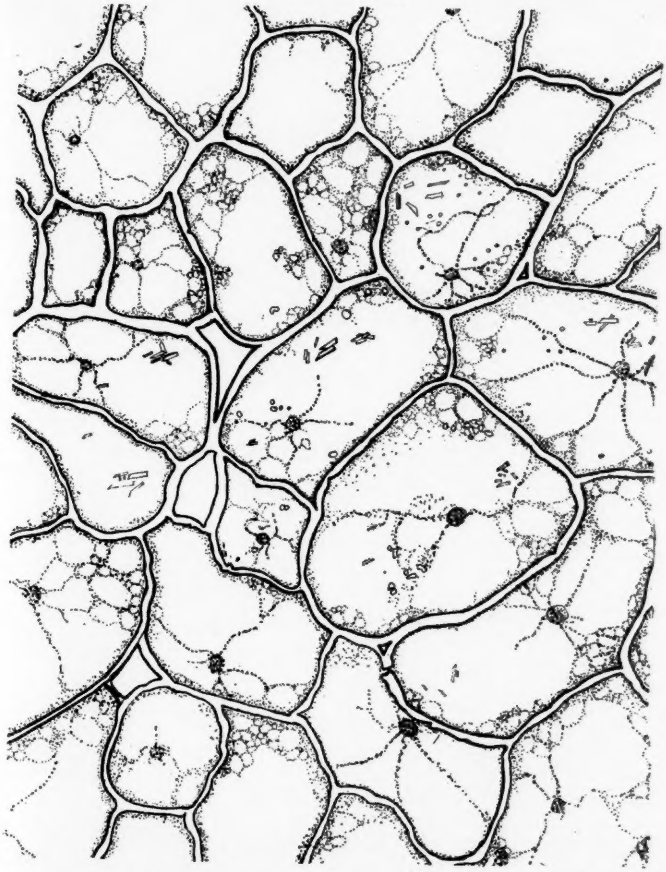


FIG. 4. Basal cells over one hundred years old in cross section × 122, 399 × 265 microns.

a notable proportion of elements which have been converted into vascular tissues, which with their heavy cellulose walls would increase the proportion of solid material. It was impossible to make a separation of masses of parenchyma cells to obtain data directly comparable with the figures given above. It was found, however, that masses of parenchyma and wood included about 89 per cent. water and 11 per cent. solid matter. Any reasonable esti-

mate of the part of the dry weight which constituted 11 per cent. of the whole would support the inference that the actual structure of the parenchymatous cells had not received any notable accretion. What may have been received may be attributed to depositions in the walls which are visibly heavier. Decreased depression of freezing point of sap does not prove diminished material in solution, but taken in connection with formations seen with the microscope suggest loss of mucilages from solution and gel structures in the protoplast. Something of the nature of these losses is revealed by the auxographic records discussed below.

Sap was expressed from portions of the medulla taken from the apical, median and basal regions of a trunk 8 m in height cut down on March 8, 1926. Freezing point determinations were made with a Beckmann thermometer and the following data obtained by Dr. F. H. Long, to whom I am indebted for the titration results given below.

Region	Depression of freezing point in degrees Cent.	Calculated as osmotic pressure in atmospheres
Apical	0.655	7.9
Median level	0.580	7.0
Basal 0.5 M level	0.565	6.8

The gradations in freezing point of the sap of the medulla are seen to be consistent and to be parallel to the disappearance of the mucilages. The direct conversions of these figures into osmotic values as given has but small value, since analyses not to be given in detail here show that the proportion of sugars determined as glucose increases from the apex toward the base. The actual suction capacity of these basal cells may be greater than in the apical region.

Cell-masses from the regions in question when placed in water and in watery solutions would satisfy the water deficit to an amount affected and determined by the action of the substances in solution. The change in volume of cell-masses under an auxograph would be determined by such increase and also by the increase resulting from the

suction power of the colloidal mass of the protoplast and wall.

Numerous measurements of the changes in volume of sections of Opuntia have been made in the last ten years and it has been shown that the living cell-masses of the flat joints of this plant have a sap which is buffered at about Ph 4. The total acidity varies as much as 4 or even 7 to 1 during the day. The greatest distention in the maximum acid condition took place in solutions at Ph 2.5 and in the acid depleted condition in solutions at Ph 3. The greatest distention on the alkaline side of neutrality took place in hydroxides at Ph 12.

Titrations of the expressed sap of Opuntia by Richards[4] showed that the total acidity was greatest in the morning and decreased until about 4 p. m. The amounts of KOH 0.1N necessary to neutralize 1 ml sap at 9 a. m. being 1.45 ml, at 12 M 0.95 ml and 4 p. m. 0.53 ml.

Similar titrations of the cortex of Carnegiea in April, 1911, required 0.91 ml. KOH 0.1N to neutralize 1 ml sap taken at 9 a. m., 0.74 ml at noon and 0.50 ml at 4 p. m., the total acidity being thus less than that of Opuntia, although undergoing a wide daily variation.

Titrations of sap taken from the base and apex of the medulla of a tree cut at 8 a. m. and extracted twenty-four hours later by Dr. Long showed that 0.256 ml KOH 0.1N was necessary to neutralize 1 ml sap from the apex and 0.144 ml sap from the base. The medulla being deeply imbedded probably undergoes very little diurnal change. The chief point of interest is the greater acidity of the young apical cells and the low acidity of the century-old basal medulla.

Another tree was felled at 7 a. m., April 6, 1926, basal and apical sections a meter in length wrapped and brought into the laboratory and the sap titrated at 10 a. m. Despite care used the extreme tip had become blackened by the action of peroxidases and sap from this part required 0.385 ml KOH 0.1N to neutralize 1 ml. Sap

[4] Richards, H. M., "Acidity and Gas Interchange in Cacti," Publ. 209 Carnegie Inst. of Wash. 1915. p. 46.

taken from cell-masses 30 cm from the tip required 0.424 ml of the KOH solution. Sap from the basal section a meter from the base of the tree required 0.144 ml of the KOH solution while that of the lowest cells available used but 0.136 ml. The figures from basal cells are not widely different from those obtained from the first tree examined, while the data from the apical region suggest rapid breaking up of acids.

The sap of the cortex of Carnegiea has been seen to be buffered about Ph 4, and a year ago it was found that slices of living or dead cells in this condition showed the greatest distention in acid solutions at Ph 3.5. The greatest increase on the opposite side of neutrality was found between Ph 10 and 12.[5]

It was not possible to make H-ion determinations of sap from freshly cut material, but extractions were made from the central part of large masses taken from trees felled three days previously, by Dr. B. L. Clarke. No difference could be found in the sap from the apical region and that from the base under such conditions, both standing at Ph 5.5. This H-ion concentration is one characteristic of the mucilages of the cacti and the figures suggest the absence of malic or other acids which might be expected. The H-ion concentration of the medulla is thus much less than that of the cortex.

Hydration of Young and Old Medulla

When slices of medulla are placed under the auxograph and treated with water or watery solutions, water will be taken up and the volume of the suction increased to an amount determined by the water deficit, the osmotic value of the sap, the suction power of the plasmatic colloids and by the permeability. The progressive swelling of the cells finally reaches a maximum at which permeability increases to permit escape of liquids from the cell by filtration pressure set up by the stretched walls.

[5] MacDougal, D. T., "Absorption and Exudation Pressures in Plants," Proc. Amer. Phil. Soc. *54*, 102–130, 1925.

As will be shown below sections arranged to measure expansion in a radial or tangential plane showed greatest increase in a radial direction in young cells and in the longitudinal axis of the tree in the older basal medulla. The material treated was taken to illustrate the action of cell-masses from the apical, intermediate and basal regions of trees of various sizes so that, for example, twenty-five-year-old cells would be found in the base of some plants and in the upper third of the trunk in others, thus eliminating variations due to position in stem irrespective of age. The first test was arranged to measure expansion of basal cells in a longitudinal direction and of apical cells in a tangential direction.

Radial slices from both regions were desiccated to obtain the expansion of the dried material in a tangential direction. Such slices from the apical region came down to about one tenth of the original thickness, while those from the basal part reduced to about one fifth of the original. The comparative expansion of the dried slices from the basal region is therefore obtained by adding 16 per cent. to the estimates of expansion estimated on the original thickness and 100 per cent. estimated on the dried thickness of the sections. The various estimates are given below (Table 1).

TABLE I

BASAL

	Living sections Percentages of original thickness Longitudinal	*Dried sections* Percentages of original thickness Tangential	Percentage of dried thickness
Water	4.3	48	205
KOH 0.01N	5.5	41	188
HCl 0.01N	4.2	49	208
$CaCl_2$ 0.01M	3.3	46	195

APICAL

	Living sections Percentages of original thickness	*Dried sections* Percentages of original thickness	Percentage of dried thickness
Water	13.3	66	640
KOH 0.01N	6.2	71	686
HCl 0.01N	1.3	31	300
$CaCl_2$ 0.01M	4.0	32	311

The measurements of the living material show that the coefficient of distention of the apical material is greater than that of the basal and that the highest swelling of the apical material is in water, while the greatest distention in the basal medulla is in hydroxide, points which will be discussed further in the light of specific tests arranged to determine the matter.

The chief value of the data in Table 1 is to be attributed to the results of hydration of the dried sections. Desiccation of regular sections resulted in thin plates of leathery material from which nothing had been extracted and in which oxidation had been very slight. The principal changes may be taken to be those concerning the colloidal condition of the walls and plasmatic layers. The walls would be affected least, and the flexible condition of the sections indicated that the liquefiable pentosans and lipins included and retained a high proportion of the water of hydration. The permeability of these walls would be but slightly modified by desiccation and such modification would be one by which permeability would be lessened.

Desiccation of the plasmatic mass would mean loss of water of hydration from the protoplasmic gels and the adsorption of the salts dissolved in the vacuoles with an adsorption of these substances in a concentrated condition with resulting coagulations which would make for increased permeability. The dried cell would therefore have walls less permeable than in the living cell and with plasmatic layers more permeable. The osmotically active substances which would be sugars would remain unchanged.[6]

The apical region is rich in sugars, especially the pentosans, and as all masses of young rapidly growing cells are high in lipins the presence of these substances may be assumed. The mucilaginous substances have largely disappeared from the basal region a matter which may be observed simply by handling freshly cut medullas. The

[6] See MacDougal, Richards and Spoehr, "Basis of Succulence in Plants," *Botan. Gazette*, 67, 405–416, 1919.

plasmatic mass in the younger cell may be taken therefore to be a protein-pentosan-lipin colloidal mixture and as such would show its greatest distention in hydroxide at the concentration used and its least in acid and in calcium solution.

The pentosan component of the plasmatic mass has largely been converted into solid wall in the older cell, with the result that the plasmatic mass is relatively higher in protein and with less lipins or phosphatides. The depreciation of the colloidal mass would give these cells a distention capacity less than in dried sections of young material with a maximum in the acid solution and a minimum in the hydroxide.

A series of tests was now arranged to determine the distention of living cell-masses in various solutions with respect to the H-OH concentration. Sections arranged to show longitudinal variations in basal and apical cell-masses were taken from a tree 6 m in height and placed in solutions under auxographs with increases given in percentages of original thickness as follows:

TABLE II

	Basal	Apical
HCl 0.005N	15.0 p. ct.	8.7 p. ct.
" 0.001"	16.4	11.
0.0002N	14.6	11.
Water	11.4	*16.7*
KOH 0.0002N	*13.3*	15.5
0.001	12.6	14.
0.005	12.6	16.

Another set was based on material taken from a tree 5 m in height. Longitudinal variations in percentages of original thickness were as in Table III:

TABLE III

	Basal	Apical
HCl 0.005N	22 p. ct.	3.5 p. ct.
0.001	23	3.8
0.0002	23	4.
Water	17.5	*4.5*
KOH 0.0002N	20.	4.0
0.001	21.	5.2
0.005	22.	5.5

It is obvious that in young cells any modification of the H or OH concentration away from the neutral as in water is followed by increased permeability as denoted by lessened swelling or distention. The hydroxide at 0.001 to 0.005N (about Ph 10–11) causes a decrease by well-known effects on the colloidal materials of the plasma and walls, but such concentrations are far beyond the biological range of experiences of the material. Increasing permeability and cessation of swelling follows immersion in graded concentrations of the acid.

The basal regions present a set of reactions with a different aspect in which effects the predominance of pro-

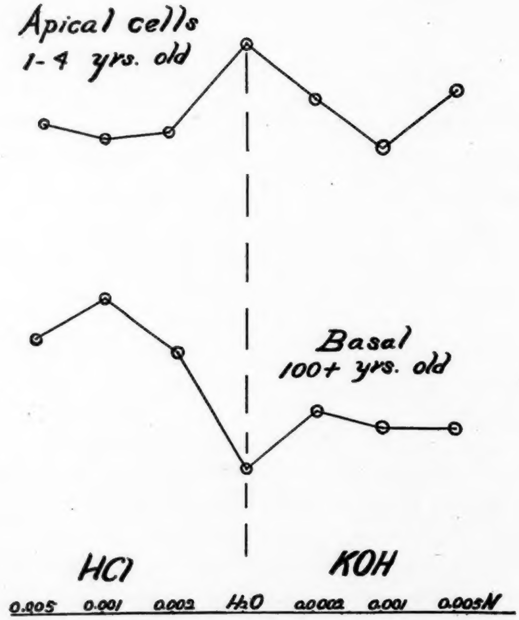


FIG. 5. Diagrams showing relative distention of young apical cells and century-old basal cells in water and in graded concentrations of acid and alkaline solutions. The greatest distention of young cells takes place in water or in a slightly alkaline solution. Permeability is not lessened in strong alkaline solution. Old cells show least permeability in acid at Ph 3 and a second maximum in alkali at about Ph 9–10.

teins in the cell-colloids is suggested. Here the maximum swelling is in acid in the region of Ph 3–3.5. A second maximum is found on the opposite side of neutrality in the region of Ph 9–12. (See Fig. 5.)

The ages of the two trees from which material was taken for the two tests the results of which are given above may be estimated at sixty to seventy-five years. The basal cells had reached a condition in which hydration reactions with respect to the H–OH concentration was similar to those of the oldest cells.

Another set of measurements was made with sections taken from a tree 9 m in height in which the oldest basal medullary cells would be well over a century old. Sections from a region about 75 cm from the apex in which the medullary cells were about eight to ten years old, others from a region about 3 m from the base and hence about fifty to sixty years old and a third lot from the basal end of the medulla with an age well over a century were tested in various solutions. The increases in percentages of original thickness are given in Table IV.

TABLE IV

Solutions	Apical		Median		Basal	
	Long.	Tang.	Long.	Tang.	Long.	Tang.
HCl 0.005N	6.	4.4	12.	3.5	3.	1.0
0.001N	7.	4.5	10.	3.8	*9.*	1.0
0.0002N	4.	6.0	12.	*5.*	5.	*1.5*
Water	5.3	6.5	*12.5*	5.8	7.	*1.5*
KOH 0.0002N	7.	*7.0*	12.	5.	5.	0.8
0.001N	*9.*	*7.0*	11.	4.3	5.	0.7
0.005N	4.	5.6	*14.*	*5.*	......	1.0

The cells of the apical region used in this test had an age of eight or ten years and had attained a condition in which the longitudinal increase in the acid solution at 0.001N and in the alkaline solution at the same concentration was greater than in water. It is to be remarked, however, that similar determinate reactions were not apparent in cell-masses supposedly fifty or sixty years old in the median region. Hydration of the medulla of this region was affected but little by the presence of acids or alkali, and this in a manner not readily explainable.

Cells of the basal region gave reactions described above as characteristic of old cells. The greatest distention took place in the longitudinal axis with the maximum on the acid side at about Ph 3 with a second maximum on the alkaline side in the region of Ph 10 to 12, which is well beyond the range of biological possibility. The expansion in the tangential direction was so slight as to give but little opportunity for differential action, but the swelling in acid of low concentration was equivalent to that in water.

A final series of tests were made with material from the medulla of a tree but 2 m in height and hence about twenty-five to thirty years old. Apical material was taken from the terminal region formed during the previous year (1925). Basal sections were of material of an age a few years less than that of the tree.

Sections from the apical region showed a distensibility of 7.5 per cent. in the longitudinal axis in water and 25 per cent. in a tangential plane. Here as in all other tests of cell-masses one and two years old any departure from neutrality in the solution resulted in a distention less than that in distilled water, a result which is ascribed to increase in permeability as noted above.

Sections from the basal part of this tree, which may have been about twenty years old, were measured as to the longitudinal and tangential expansions, which were as follows:

TABLE V

Solutions	Longitudinal	Radial
HCl 0.005N	16.0	2.0
0.001	18.0	3.5
0.0002	16.5	3.5
Water	15.5	4.5
KOH 0.0002	16.0	3.0
0.001	16.0	2.0
0.005	18.0	2.0

The differences in distention in the various concentrations were irregular and of small amplitude, the whole set of reactions denoting that this part of the medulla

was approaching the second stage of distention in which a maximum was shown in acid at about Ph 3.

Discussion

The medulla of the sahuaro (*Carnegiea gigantea*) is composed primarily of parenchymatous cells which may retain their meristematic condition during the life of the tree, one hundred to one hundred and fifty years. Some cells are converted into vascular tissues, forming anastomosing strands connected with the enclosing woody cylinder. All the basal part of the medulla for a length of 20 to 30 cm is so converted.

The central position of the medulla and its enclosure in the woody cylinder which is in turn sheathed by a thick succulent cortex insures it against changes in environmental agencies of high rate or great amplitude. The most pronounced changes to which the medulla is subjected are those of temperature. It has been found that the tree can not survive in localities where the air-temperature may remain below the freezing point for an entire day, although it endures the repeated occurrence of freezing temperatures a few hours in the morning. This would imply that the cells endure about 2° C as a low point, while other data would lead to the inference that the medulla may at times be as high as 45° C. Some metabolic activity would take place over this range, although it is to be noted that the actual growth in the apical region does not continue below 10 to 12° C: the upper limit has not been determined, but it may be taken as not widely different from that of Opuntia (58° C).

Growth, or distention of the cells, may take place during periods of about 150 days each year. That this is repeated each year for the first half century is demonstrated by the measurements. The increase during the second half century is even more marked.

Dimensions of cells of various ages are indicated by their areas in cross and longitudinal sections as follows:

Young cells	Long.	Transverse
	246 x 188 microns	249 x 206 microns
50 years old	272 x 224	256 x 226
100 " "	322 x 196	399 x 266

The areas of cells seen in cross-section had increased as from 513 to 579 at the end of the first half and to 1,061 at the end of the century. In longitudinal section the increase was as from 463 to 609 at the end of fifty years and 739 at the end of the century. The greatest distention is seen to be radial in a plane at right angles to the axis of the tree.

Distention in the plane exposed in the longitudinal section was nearly as great in the second half century or more as in the first being as 130 to 146. Distention in a plane transverse to the axis of the tree was greater in the second period or more than in the first being as 482 to 66. The graph in Fig. 6 has been constructed from these data.

The long course of life of these medullary cells is attended by an increase in glucose, a decrease of mucilages or pentosans in the sap and in the plasmatic gel coupled with a thickening of the cell wall suggestive of direct conversion of deposition of these carbohydrates.

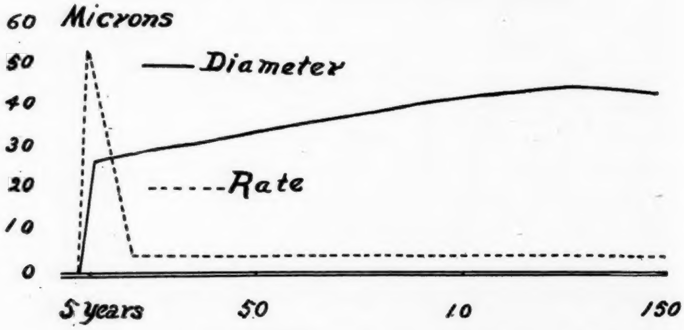


FIG. 6. Diagrams showing varying size and rate of growth of medullary cells of sahuaro for 150 years. Size is plotted directly from measurements indicated by the averages under Figs. 2, 3 and 4. The graph representing the rate is calculated on the assumption of rapid growth continuing for five years. It is probable that this high rate is held for one year only.

Even more notable is the difference in swelling or hydration reactions of young and century old cells. Sections of young cells immersed in a series of graded concentrations of acid and alkali show increased permeability and lessened swelling by a departure either way from neutrality, the depression being least pronounced on the alkaline side. At extremes of concentration, action is reversed.

The changes in volume in old cells are markedly different from those of young cells. The lessened extensibility of the heavily thickened walls[7] now limits expansion and lessens permeability and the protoplasts in which proteins now predominate show two isoelectric regions in which permeability is least and swelling greatest. These effects were obtained in solutions at Ph 3–3.5 and at Ph 10–12. These maxima are not widely different from those found in active cortex of Carnegiea, the sap of which is buffered at about Ph 4. The sap of the cortex is maintained near the region of possible maximum turgidity, while that of the medulla is widely away from it. It is notable that these results show but little connection between proportionate H-ion concentration of the sap and that of the immersing solution, in the effect produced on distention of swelling.

Other interesting inferences would be to the effect that proteins associated with cellulose in the wall in the early stages disappear or pass into the plasma, while the lipins or phosphatides so richly present in the young protoplast would be combined with calcium or be absorbed into the wall.[8]

On the basis of fact and these appended assumptions the wall of the young cell high in liquefiable pentosans

[7] See Krassnosselksky-Maximov, T. S., "Untersuchungen über Elastizitat der Zellmemhau," Ber. d. deut. Bot. Gesell., 43, 527–537, 1926.

[8] See MacDougal, D. T., E. R. Long and J. G. Brown, "End Results of Desiccation and Respiration in Plants," Physiol. Researches, No. 6, 1915, Baltimore, and Tupper-Carey, R. M., and J. H. Priestley, "The Composition of the Cell Wall at the Apical Meristem of Stem and Root," Proc. Roy. Soc., B., vol. 95, 109–131, 1923.

and glycoproteins would be highly permeable and the protoplast much less so.

At the end of a century, the protoplasts shrunken by loss of pentosans, and lipins would be highly proteinaceous with more glucose, would include a great number of crystals and would be more permeable. The walls, on the other hand, would be thickened by deposition, while their changed composition would render them less permeable.

Changes in volume in various solutions as measured by the auxograph would be a resultant of the water deficit of the material when tested, the suction power of the colloids in wall and plasma, their permeability and the extensibility of the walls.

It is notable that the H-ion concentration of the sap does not vary widely during the life of the cell, that it is within the range of a solution of mucilages or pectins and that it is much less than that of the surrounding cortex.

SUMMARY

(1) Cells of the medulla of *Carnegiea gigantea* may continue to grow for nearly a century and to be active until the death of the tree.

(2) Parenchymatous cells of the medulla retain their meristematic condition during the longer period mentioned.

(3) Great numbers of parenchymatous cells of all ages are transformed into vascular bundles forming strands connecting with the woody cylinder.

(4) The estimated rate of enlargement of medullary cells is greater in the second than in the first half century, following the initial distention.

(5) Growth occurs within periods of 150 days annually.

(6) Environmental conditions are favorable to activity except for a few periods of a few hours duration of low temperature each year.

(7) Pentosans or mucilages abundant in young cells diminish with age.

(8) Glucose content increases with age.

(9) Silica crystals become more abundant with age.

(10) Plasmatic layers shrink with age and become granular, while the nuclei change but little.

(11) Cell walls become thickened with age.

(12) The H-ion concentration varies only within narrow limits, Ph 5.3–5.7, which is about that of a pectin or pentosan solution.

(13) Fatty substances are abundant in young cells in winter, their disappearance being followed by the appearance of starch in young cells.

(14) Immersion of young cells in acid or alkaline solutions increases permeability and diminishes water-holding capacity of young cells.

(15) Similar immersion of old cells in graded concentrations is followed by maximum swelling in acid solutions at Ph 3 to 3.5 and a secondary maximum in alkali at Ph 9 to 11. Such nodes have been attributed to the influence of isoelectric regions of proteins in Opuntia. The possible effects of variations in composition of the wall with age were not tested.


Dr JOHN HILL.
F. Cotes ad Vivum del. 1757
R. Houston Fecit

THE VERSATILE SIR JOHN HILL, M.D.

PROFESSOR LORANDE LOSS WOODRUFF

PROFESSOR OF PROTOZOOLOGY, YALE UNIVERSITY

THE eighteenth-century in London was a period of contrasts. The town had developed quite suddenly a new method of living, social intercourse being the dominant note with its outlet in drum and rout, coffee house and tavern, Vauxhall and Ranelagh. The ostentatious display of a Chesterfield brought into relief the unkempt personality of a Johnson. On the intellectual side, with all due respect to the Lord and the Doctor, those who have recently been appropriately dubbed the "Fifth Estate"[1] were diligent investigators in a largely unexplored field. The previous century, as exemplified by Robert Hooke's "Micrographia,"[2] had demonstrated the profit of studying nature with mechanical aids to the senses and instruments of precision, and the furrows it turned were being slowly seeded and the first products garnered. The contrast between the man of science and the man of the street was probably never so great—and both extremes were embodied in Sir John Hill, M.D. Dr. Hill is a type which we always have with us, but the London of his day afforded free play for his versatility as apothecary, astronomer, actor, botanist, microscopist, mineralogist, zoologist, physician, editor, journalist and man of fashion. One has but to turn the pages of London's print from 1750 to 1775 to meet his name.

John Hill was the second son of the Rev. Theophilous Hill and was born in 1716 or 1717 either at Peterborough or Spalding. Little is known regarding his early education, except that it did not include formal academic work,

[1] A. D. Little, "The Fifth Estate," *Science*, 60, 1924.

[2] L. L. Woodruff, "Hooke's Micrographia," AMER. NATURALIST, 53, 1919.

and we first find him apprenticed to an apothecary, as was not unusual at the time for those who planned to practice medicine. But lectures on plants which he attended at the Chelsea Physic Garden apparently gave him an unusually broad botanical foundation, and it was this knowledge that he immediately attempted to capitalize when in his early twenties he found the income from his own apothecary shop in St. Martin's Lane unequal to the needs of a growing family. He traveled extensively in England, collecting plants which he dried and arranged in sets with classifications and descriptions. Sufficient subscriptions to the *hortus siccus,* however, were not forthcoming, and after some horticultural work for certain of the nobility he forsook temporarily the profession of herbalist for that of actor.

Hill's appearance at the Haymarket and Covent Garden was apparently equally unprofitable from the standpoint of his finances and his reputation, if we may judge from amusing accounts given by his contemporaries; but this did not deter, indeed, probably inspired him a few years later to publish anonymously a stout little volume entitled "The Actor; a Treatise on the Art of Playing, Interspersed with Theatrical Anecdotes, Critical Remarks on Plays, and Occasional Observations on Audiences." And this he dedicated "To the Managers of the Two Theatres." That it attracted attention at the time is clear by the quarrels in which it involved its author, and these were accentuated later by two mediocre plays[3] whose failure Hill attributed to various actors, with whom he exchanged uncomplimentary epigrams. Garrick wrote:

> "For physic and farces his equal there scarce is;
> His farces are physic, his physic a farce is."

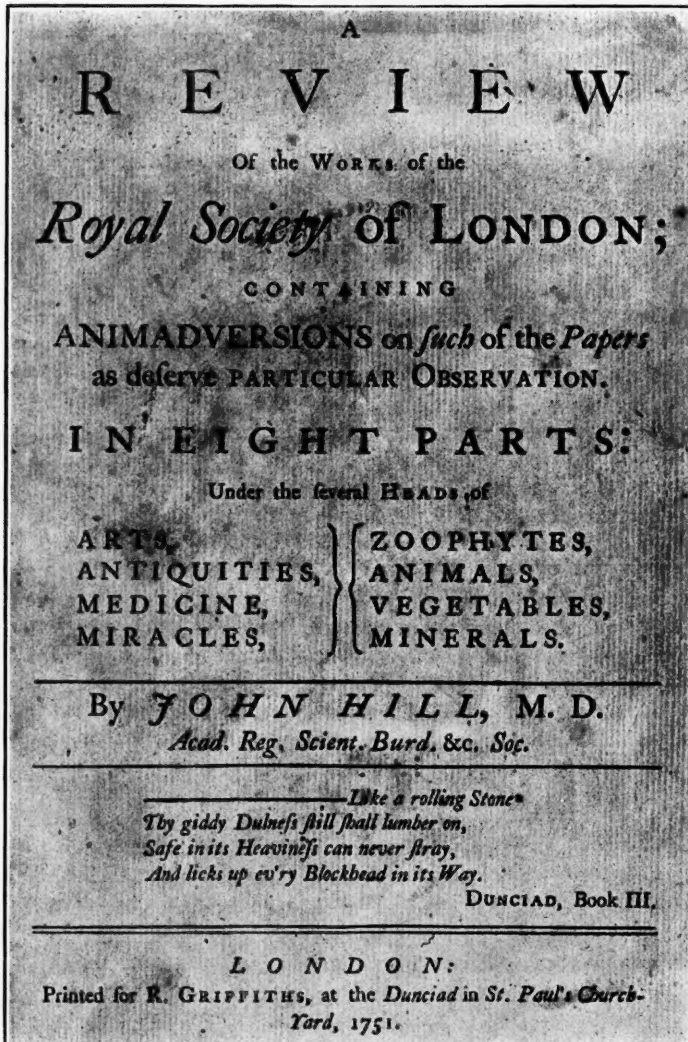
Sensing at once that the stage of the time offered nothing, Hill resumed his practice as apothecary and physi-

3 "The Maiden's Whim" (1756); "The Rout" (1758). As early as 1740 he wrote an opera, "Orpheus." *Cf.* D. E. Baker: "Biographia Dramatica," London, 1812 edition, pp. 341–348.

cian, fortified by a medical degree granted, *in absentia*, by St. Andrews. The available evidence indicates that he was not unsuccessful, for in 1746 we find him acting as a regimental surgeon, with time to edit the *British Magazine* and to publish a translation of Theophrastus's "Treatise on Gems" with additions and critical notes which considerably increased its contemporary interest and value. Where Hill secured the knowledge which enabled him to annotate successfully this work, which was revived eight years later in a French translation, remains an enigma, but it is only the first of a long series of surprises that Hill affords as his career proceeds. At all events this essay in the field of science brought him to the favorable attention of certain eminent fellows of the Royal Society, in particular Martin Folkes, president of the society, and Henry Baker,[4] the well-known microscopist, who for a time accorded him their patronage.

Stimulated, indeed, over-stimulated by this success, Dr. Hill now turned chiefly to his pen for his fortune and produced during the remainder of his life upward of eighty publications, not a few of which were in large folio. But such a statement gives no adequate idea of his prodigious capacity for work—"this gentleman may very justly be estimated as a phenomenon in literary history,—he was perhaps one of the most voluminous writers that this or any other age has produced." At one time he was engaged upon as many as seven volumes. Almost all branches of literature were included—fiction, the classics, theology, history and science; one or more volumes being devoted to astronomy, zoology, husbandry, botany, gardening, microscopy, medicine and the conduct of married life. In brief essays contributed daily for more than three years to the *London Advertiser*, under the pseudonym of *The Inspector*, there is hardly a phase of contemporary life or problems which he avoided. True, the inspector was primarily a monger in small

[4] L. L. Woodruff, "Baker on the Microscope and the Polype," *Scientific Monthly*, 7, 1918.



A

REVIEW

Of the WORKS of the

Royal Society of LONDON;

CONTAINING

ANIMADVERSIONS on *ſuch* of the *Papers*
as deſerve PARTICULAR OBSERVATION.

IN EIGHT PARTS:

Under the ſeveral HEADS of

ARTS,	ZOOPHYTES,
ANTIQUITIES,	ANIMALS,
MEDICINE,	VEGETABLES,
MIRACLES,	MINERALS.

By *JOHN HILL*, M. D.
Acad. Reg. Scient. Burd. &c. *Soc.*

——————Like a rolling Stone
Thy giddy Dulneſs ſtill ſhall lumber on,
Safe in its Heavineſs can never ſtray,
And licks up ev'ry Blockhead in its Way.
DUNCIAD, Book III.

LONDON:
Printed for R. GRIFFITHS, at the *Dunciad* in *St. Paul's Church-Yard*, 1751.

things, but this prototype of the columnist rises, now and again, distinctly above mediocrity in his daily output, especially when discussing natural history subjects.[5] Some of the Inspectors are of particular interest because they show that Hill was in many ways ahead of his times. One, for instance, suggests that botany would be greatly advanced by the delivery in the museum of public lectures illustrated by living plants—a foreshadowing of the laboratory method in biology; while another mentions the relationships of insects to pollination—a decade before Koelreuter. But, be their intrinsic value what it may, the daily grind was profitable to him in more than one way; it made him well known to the public, netted him a small fortune, and involved him in various quarrels with Garrick, Fielding, Smart and other literary men of the time —all of which was apparently to his liking.

It so happens that the contemporary estimate of Dr. Hill is chiefly preserved for us by the literary fraternity with whom he soon found himself at odds, and accordingly it is not surprising that his failings are not minimized and his virtues are largely overlooked. And the modern biographers of his associates accept unchallenged these estimates of the doctor-opponent of their paragons.[6] Nearly all find it necessary, for example, to recount at length the war of words between The Inspector and Fielding in his *Covent-Garden Journal*,[7] and to award the palm of victory to Fielding—after the lie had been passed—for his reply in which he refers to the doctor as "only a little paltry dunghill." Hill was not a match for the literary "giants" whom he inspected, though he was far from "losing his spirit in encountering the wits,"[8] and any one who will read without prejudice

[5] "The Inspector." Reprinted with omissions and corrections, London, 1753.

[6] *Cf.* Frederick Lawrence, "Life of Henry Fielding," 1855; W. L. Cross, "The History of Henry Fielding," 1918.

[7] G. E. Jensen (editor), "Fielding's Covent-Garden Journal." Yale University Press, 1915.

[8] Isaac Disraeli, "Quarrels of Authors," London, 1814.

the best of his essays and compare them with the average output of his contemporaries can not fail to credit Hill with no mean literary ability.

Samuel Johnson's fling at Dr. Hill took place, it will be recalled, when Johnson was reading in the King's Library and His Majesty, entering, began to interrogate him. Boswell gives it impressively:

> The King then asked him what he thought of Dr. Hill. Johnson answered, that he was an ingenious man, but had no veracity; and immediately mentioned, as an instance of it, an assertion of that writer, that he had seen objects magnified to a much greater degree by using three or four microscopes at a time than by using one. "Now," added Johnson, "everyone acquainted with microscopes knows, that the more of them he looks through the less the object will appear. . . ." "I now," said Johnson to his friends, when relating what had passed, "began to consider that I was depreciating the man in the estimation of his Sovereign, and thought it was time for me to say something that was more favorable." He added, therefore, that "Dr. Hill was, notwithstanding, a very curious observer; and if he would have been contented to tell the world no more than he knew, he might have been a very considerable man, and needed not to have recourse to such mean expedients to raise his reputation."[9]

Whether Johnson's magnanimous final remarks, which amounted to reiterating that Hill was a liar, raised Hill in the estimation of his sovereign, does not appear, but the whole episode makes it clear that the King and Johnson were talking about something of which they knew nothing. Certainly "if Hill's reputation for lying rests on no surer foundation than this, he must be acquitted of much that is charged to him."[10] Of course, Dr. Hill was referring to lenses combined in the recently developed compound microscope. He himself had made certain minor improvements in the microscope which were embodied in an instrument offered for sale by the well-known London instrument maker, George Adams. Complete specifications with illustrations were given by Hill in his volume on "The Construction of Timber" (1770), and these were copied verbatim in the fourth edition (1771) of Adams's "Micrographia Illustrata" with-

[9] James Boswell, "Life of Samuel Johnson."

[10] T. G. Hill, "John Hill," in "Makers of British Botany," F. W. Oliver, editor, 1913.

out so much as mentioning Hill. But this did not trouble Hill—he was well able to look out for himself. As one of the many epigrams which showered him put it:

> Hill puffs himself; forbear to chide!
> An insect vile and mean
> Must first, he knows, be magnified
> Before it can be seen.[11]

Not content with arousing a storm among his literary contemporaries, Hill also raised consternation in the ranks of his scientific colleagues which reached its height when he made his famous attack on the Royal Society. It is not at all clear what gave rise to this onslaught since the various accounts do not agree. Hill attributed it to the perfidy of one of the fellows who, while calling at his house, took the liberty of reading a letter which Hill had written and left unsealed on his table. It appears, according to Hill, that a French correspondent, supposing him to be a fellow, had taxed him with "one of the errors of the Society," and Hill's letter stated, "I have already set right the error you complain of; but you are to know that I have the honor *not* to be a member of the Royal Society of London."[12]

Be this as it may, there is reason to believe that Hill became a candidate for election, since his publishers desired an F. R. S. after his name on their title pages, and failing of election because he had referred to various fellows as "cockelshell merchants," "medal scrapers" and "butterfly hunters," he launched a series of attacks including his indecent "Lucina sine concubitu" in 1750 and the following year his "Review of the Work of the Royal Society of London," both enjoying wide popularity in England and on the continent.[13] The latter appeared in the form of the *Philosophical Transactions,* and, after a rather lengthy preface, takes up about eighty papers published by the society. That animosity lurks in the au-

[11] *Cf.* Disraeli, *loc. cit.*
[12] Preface, Hill's "Review."
[13] *Cf.* Hill's novel, "Adventures of Mr. George Edwards, a Creole," 1751.

thor's mind is apparent from the dedication to his former patron, the president of the society, for Hill writes:

It is to you alone that the world owes their having been written; the purport of the more considerable of them [the criticisms] has been long since delivered to you in conversation; and if you had thought the Society deserved the censure that must attend this method of laying them before the world, you might have prevented it, by making the necessary use of them in private. Nor is this, Sir, the only sense in which you have been the great instrument of their production; since it cannot but be acknowledged, that if anybody, except your great self, had been in the high office you so worthily fill at present, the occasions of many of the more remarkable of them could not have been received by the body, under whose countenance alone they claim their places in this work.

And Hill in the course of his preface modestly justified his method of treatment and his competence to criticize some of the learned fellows by stating that "if he is merry in some places, let it be considered, that the subjects are too ridiculous for serious criticism; if he is positive in others, let it not appear too assuming; he pretends to nothing but the knowing more than the Royal Society of London appears by its publication to know, and surely a man may do that, and yet be very ignorant!" However, he specifically states that "among the members of it, there are men great in all senses of the world, men esteemed in the highest degree by the author of these animadversions, and by whom he thinks it has greatest honor to be esteemed. . . These see too clearly to suppose a censure of the society under its present management, an attack upon their separate characters."

Two facts are clear from this Review. First, that Hill exhibits considerable ability as a literary opponent—his biting sarcasm and irony, frequently couched in happy phraseology, was never to be forgotten by the recipients of the thrusts. Second, that its author was one of the best informed scientific men of his day, who, from the standpoint of his actual scientific accomplishments, was far more worthy of honor than some of the fellows. And Hill knew it.

The opening paragraph of the Review is sufficient proof that the doctor had much fun—albeit a bit unfair—at the expense of the papers:

A Way to Kill Rattlesnakes.—The ingenious author of the paper, in which this societarian method of destroying these poisonous and terrible animals is published, is Capt. Silas Taylor. It is indeed a kind of martial achievement, and worthy the title of the man who gives it; and as we dare venture to affirm that it will take place as well upon our own poisonous serpents, as on those of America, we could not omit giving it a conspicuous place, in a work intended like this of ours, for the general benefit of mankind. The method is delivered so early as in the third number of the *Philosophical Transactions*, and runs thus: Catch a rattlesnake, as large and vigorous as you please; fix it in any manner that you will, so that it cannot possibly get away; then procure a cleft stick, and put into the notch of it a quantity of the bruised leaves of wild pennyroyal; direct the end of the stick towards the serpent's nose; as he avoids it, still pursue him with it; and in half an hour's time he will be killed by the mere scent of the herb. . . . If the world should wish to see this amazing discovery paralleled by another more modern instance, we have a very late one in a countryman of our own, the ever to be remembered inventor of the powder for killing of fleas. The method of using this was very like that which the Captain here prescribes for his pennyroyal. The flea was to be held conveniently between the thumb and finger of the left-hand, while a very small quantity of the powder was applyed to the end of its trunk; after which, if the same flea could be proved ever to have bit the person again, he was to have another paper of the powder for nothing. How unhappy was it for the ingenious inventor of the method of destroying these vermin, that he did not apply himself to the Royal Society! The very first old woman he sold a paper to, unluckily asked him, whether, when she had got the flea, if she should crack it under her nail it would not be as well? The poor fellow could not but answer, that that way would do too, and was so thunderstruck with the objection that he never sold another. Such is the misfortune of a man's applying himself to old women, and being upon the spot, and in the way of having impertinent questions asked him: had he lived in New England or Virginia, and only communicated his discovery to a Royal Society, who of all its members would have thought of such a trifling objection to so useful a proposal?

And then Hill proceeds from paper to paper. One describes "a way to make all sorts of trees, plants, and fruits grow to an extraordinary bigness"—"sow the seeds or kernels, at the very instant when the sun enters into the vernal equinox," and "transplant them precisely at the moment when the moon is full"; another suggests "a way to make smelts grow to an extraordinary small-

ness"—"take the fish out of water which affords them a great deal of nourishment, and put them into such as affords them but a little,"[14] and so on. Although Hill asserts "that the work might not be without its real use, an error is not here exposed without the establishing of

A GENERAL

NATURAL HISTORY:

OR,

NEW and ACCURATE

DESCRIPTIONS

OF THE

Animals, Vegetables, and Minerals,

Of the DIFFERENT

PARTS of the WORLD;

WITH

Their VIRTUES and USES, as far as hitherto certainly known, in MEDICINE and MECHANICS:

ILLUSTRATED

By a GENERAL REVIEW of the Knowledge of the Ancients, and the Discoveries and Improvements of later Ages in these Studies.

INCLUDING

The HISTORY of the *MATERIA MEDICA, PICTORIA,* and *TINCTORIA,* of the Present and Earlier AGES.

AS ALSO

OBSERVATIONS on the neglected Properties of many valuable Substances known at present; and Attempts to discover the lost Medicines, *&c.* of former Ages, in a Series of Critical Enquiries into the *MATERIA MEDICA* of the Ancient GREEKS.

WITH

A great Number of FIGURES, elegantly engraved.

By JOHN HILL.

LONDON:

Printed for THOMAS OSBORNE, in Gray's-Inn, Holbourn.

M.DCC.XLVIII.

[14] "Review," pp. 19–21.

the truth in the place of it," in a few cases he was himself in error, but this does not detract from the humor of the situation.

Clearly the society up to the time had not sufficiently profited by the *Tatler's* observation that "their speculations do not so much tend to open and enlarge the mind, as to contract it and fix it on trifles,"[15] and the whole episode should have endeared Hill to Fielding and the literary fraternity in general, who enjoyed ridiculing the "Experimentalists." It may be recalled that in the *Covent-Garden Journal,* Fielding refers to a very extraordinary woman "who brought forth at one birth nineteen couple of rabbits, one of which having been eaten by the Royal Society and by them declared to have a most delicious relish, the breed was afterward propagated all over the Kingdom of England, were called Welsh Rabbits, and were a long time in great request."[16]

So we find Hill during the fifties and sixties of the eighteenth-century a unique London character, with a considerable income from the voluminous publications which enabled him to keep himself before the public by driving about in his chariot, making himself conspicuous at coffee houses and theaters, and stirring up a paper war when that seemed necessary for notoriety. This would seem to be enough to consume the time of any one; but not so the doctor, for he was gardener at Kensington Palace, Justice of the Peace for Westminster, official adviser on horticulture to the governors of several tropical island colonies, and nominated, if not appointed, superintendent of the Royal Gardens at Kew. This exponent of the "gentle art of making enemies" was no ordinary man. A contemporary called him "an extraordinary genius."[17] Disraeli in his "Quarrels of Authors" says: "Sir John Hill, this despised man, after all the fertile absurdities of his literary life, performed more for the

[15] *Tatler,* No. 236.

[16] Jensen, *loc. cit.*

[17] Whiston, in Nichol's "Literary Anecdotes of the Eighteenth Century," 1812.

improvement of the Philosophical Transactions, and was the cause of diffusing a more general taste for the science of botany, than any other contemporary.'' It is to Dr. Hill's actual contributions to biology that we now turn.

We have already referred to Hill's first venture in science, his edition of ''Theophrastus on Gems.'' Its success led him to undertake the publication of a ''General Natural History'' in three large volumes between 1748 and 1752. Necessarily chiefly a compilation, it gave a ''Compleat History of the Three Great Classes of Natural Bodies'' which was second to none then extant in the English language. Von Haller recognized it as a work of infinite labor and great utility.

The volume devoted to fossils need not detain us since it offers no noteworthy original contribution, but shows clearly that the author knew his subject, and his interest in it persisted, because twenty-three years later he brought out one of the first manuals on mineralogy.[18] On the other hand, the volume on plants is of considerable importance because it introduced to English botanists the Linnaean system of plant classification.[19] This was two years before Linnaeus published his ''Species Plantarum,'' and accordingly was imperfect, but Hill incorporated the later advances in his ''Eden, or Complete Body of Gardening'' (1757); ''Gardener's New Kalender'' (1758); ''Flora Britannica'' (1760); and his ''Vegetable System'' (1759–1775). The preface of ''Eden'' declares ''The study of plants has undergone many variations with respect to method; and, at present, the system of Linnaeus is universally followed. No book on gardening has been written since this absolute change in the science. . . . Those who understand plants, now call them, universally and solely, by the names of this author. . . . We shall follow the system of Linnaeus, which we shall deliver completely, explaining his terms.''

[18] ''Fossils Arranged According to their Obvious Character,'' etc., 1771.
[19] *Cf.* B. D. Jackson, ''Guide to the Literature of Botany,'' 1881.

The third volume of his "Natural History," devoted to animals, is noteworthy because it is the first work of the kind to include "accounts of the several classes of Animalcules, visible only by the assistance of microscopes." "Certainly their want of magnitude," the author points out, "does not exclude them from their rank among animated beings; yet this is the only History of Animals, in which they have been honored with a name. I have been at the pains of viewing all these by the microscope, and not according to the erroneous accounts of those superficial writers, who have seen others; but, from what appeared on that examination, I have arranged them into a regular method and given them denominations. The reader who is addicted to cavilling must not find fault with me for this. I have not changed their names, the greater part of them had none before." So Hill devotes Book I to Animalcules and attempts to classify them, coining many names which still persist—for example, *Paramecium*. It may well be doubted whether he did not overestimate his own critical study, if one can judge by certain of his figures of the Protozoa which obviously are copied from antiquated *Philosophical Transactions* of the Royal Society, and by some of his "Essays in Natural History and Philosophy," containing a "Series of Discoveries by the Assistance of Microscopes," which he published the same year. However, it can not be gainsaid that Hill was an expert with the microscope, probably second to none in England at the time, and his initial attempt to classify the Protozoa and other microscopic organisms was an important step in the right direction, which paved the way for intensive studies by other microscopists before the century closed.

Hill's other zoological work of importance is the English edition of Swammerdam's "Biblia Naturae." This monumental work of the great student of microscopic anatomy was published posthumously in Dutch and Latin under the editorship of Boerhaave in 1738, and fourteen years later appeared in a German translation, but it was

not available in English until 1758, when Hill's edition was published. Hill did the work excellently, his notes

THE

BOOK of NATURE;

OR, THE

HISTORY OF INSECTS:

Reduced to diſtinct CLASSES, confirmed by particular INSTANCES, Diſplayed in the Anatomical Analyſis of many SPECIES,

AND

ILLUSTRATED with COPPER-PLATES.

INCLUDING

The Generation of the FROG, the Hiſtory of the EPHEMERUS, the Changes of FLIES, BUTTERFLIES, and BEETLES;

WITH THE

Original Diſcovery of the MILK-VESSELS of the CUTTLE-FISH, and many other curious Particulars.

By JOHN SWAMMERDAM, M D.

WITH

The LIFE of the AUTHOR, by HERMAN BOERHAAVE, M. D.

Tranſlated from the DUTCH and LATIN Original Edition,

By THOMAS FLLOYD.

Reviſed and improved by NOTES from REAUMUR and others,

By JOHN HILL, M.D.

LONDON:

Printed for C. G. SEYFFERT, Bookſeller, in DEAN-STREET, SOHO.

MDCCLVIII.

and comments add to its value, and the numerous plates of Swammerdam's remarkable dissections are well reproduced. Both Hill and his publishers deserve great credit for this standard edition of a biological classic.

In fairness to Hill's critics, mention should be made of his "Decade of Curious Insects," which appeared, richly illustrated in color, in 1773, two years before his death. Here he is at his worst, apparently giving his imagination free play, with no thought for his reputation and all for his pocketbook, though, if the truth be told, both were now at such a low ebb that it mattered little what he did.

But Hill was primarily interested in botany, and it is in this field that his scientific talents were chiefly displayed. His recognition of the importance of the Linnaean classification, which has already been mentioned, at once shows the breadth of his knowledge and the keenness of his foresight. Hill knew his plants and appreciated that the Linnaean system, with all its faults, which he does not hesitate to point out, offered a practical means of bringing order out of the existing chaos. Hill's commentators, who have found it impossible to reconcile his praise and criticism of Linnaeus's work, apparently overlooked this statement in Hill's "Sleep of Plants," published in the form of a letter addressed to the great botanist: "If our opinions have differed, 'tis upon a single point; your arrangement of plants. In regard to that much greater article, the establishing their distinctions, and ascertaining their characters, I have always admired and reverenced you: to dispute your determinations there, were to deny the characters of nature. Free in the tribute of applause on this head, I have on the other been as open in my censures; equally uninfluenced by envy, and by fear. It is thus science may be advanced; and you will permit me to say, thus men of candour should treat one another." Indeed, many of Hill's critics were by nature incapable of appreciating such sentiments.

Hill's chief works on systematic botany, in addition to those already mentioned, are the "British Herbal, an

THE

SLEEP

OF

PLANTS,

AND

CAUSE of MOTION

IN THE

Senſitive PLANT,

EXPLAIN'D.

By. J. HILL.

In a LETTER to

C. LINNÆUS,

Profeſſor of BOTANY at UPSAL.

LONDON:

Printed for R BALDWIN in Pater-noſter-Row. M.DCC.LVII.

History of Plants and Trees, Natives of Britain, Cultivated for Use or Raised for Beauty," a folio illustrated with more than seventy-five copper plates, and "The Vegetable System, or the Internal Structure and the Life of Plants," consisting of twenty-six folio volumes of text and plates.

"The British Herbal" was an outgrowth of his earlier "Useful Family Herbal," which, as its title page states, gave practical "directions for the gathering and preserving roots, herbs, flowers and seeds; the various methods of preserving these samples for present use; receipts

for making distilled waters, conserves, syrups, electuaries, juleps, draughts, etc., with necessary cautions in giving them." But "The British Herbal" was a scholarly compendium for the botanist, gardener and apothecary in which Hill described and illustrated a very large number of plants with great accuracy, judged by the standards of botany in England at the time, and proved his ability in this field. "The Vegetable System" was started under the patronage of Lord Bute in 1759 and the twenty-sixth volume appeared in 1775, the year of Hill's death. The noble lord apparently gradually lost interest as the work progressed and the withdrawal of his financial support made the completion of the series with one thousand six hundred full-page plates a drain on the author's finances which they could not meet, though the price of the work to subscribers was 38 guineas plain and 160 guineas colored. The scope of the work may be judged by the fact that twenty-four volumes were devoted to a systematic description of British and foreign plants, and the remaining two chiefly to an outline of the history of botany, the systems of Cesalpino, Morison, Ray, Tournefort, Linnaeus and others, and to the development of plant morphology and physiology, including the effects of various physical factors on plant growth. A plate is devoted to his own experiments on *Abrus*.

Clearly, Hill had undertaken a project which was too great for one man, unless it was Hill himself, but he was turning out simultaneously volume after volume and pamphlet after pamphlet on other subjects to keep the wolf from the door. If this is borne in mind it is fair to say that it is a most remarkable work and a fitting culmination of Hill's studies in systematic botany.

But the doctor's methods of making herbals were not immune from gossip. Dr. Erasmus Darwin, the grandfather of Charles Darwin, in a letter written when a young man (1756), says: "I believe I forgot to tell how Dr. Hill makes his 'Herbal.' He has got some wooden plates from some old herbal, and the man that cleans

THE

VEGETABLE SYSTEM.

OR,

A SERIES OF

EXPERIMENTS AND OBSERVATIONS

TENDING TO EXPLAIN

The INTERNAL STRUCTURE,

AND

The LIFE of PLANTS;

Their GROWTH AND PROPAGATION;

The NUMBER, PROPORTION, and DISPOSITION

Of their CONSTITUENT PARTS;

WITH THE

TRUE COURSE OF THEIR JUICES;

The FORMATION of the EMBRYO, the CONSTRUCTION of the SEED, and the ENCREASE from that State to PERFECTION.

NCLUDING,

A NEW ANATOMY OF PLANTS.

The Whole from NATURE only.

By JOHN HILL, M.D

LONDON.

Printed at the EXPENCE of the AUTHOR,

And Sold by R. BALDWIN, in Pater-Noster-Row.

MDCCLXII.

them cuts out one branch of every one of them, or adds one branch or leaf to disguise them. This I have from my friend, . . . the watchmaker, to whom this printmender told it, adding, 'I make plants every day that God never dreamt of.' "[20] Suffice it to say that Hill, of course,

[20] Charles Darwin's introduction to E. Krause's "Life of Erasmus Darwin," p. 16.

THE
CONSTRUCTION
OF
TIMBER,
From its EARLY GROWTH;
Explained by the
MICROSCOPE,
And proved from
EXPERIMENTS,
In a great VARIETY of KINDS:
IN FIVE BOOKS.

On the PARTS of TREES; their VESSELS; and their ENCREASE by GROWTH: And on the different DISPOSITION of thofe PARTS in various KINDS; and the PARTICULARITIES in their VESSELS.

WITH FIGURES OF
Their various APPEARANCES; of the INSTRUMENT for cutting them; and of the MICROSCOPE thro' which they were viewed.

By JOHN HILL, M.D.
MEMBER of the IMPERIAL ACADEMY.

LONDON:
Printed for the AUTHOR;
And Sold by R. BALDWIN, in Pater-Nofter-Row; J. RIDLEY, in St. James's-Street; J. NOURSE, T. BECKET, P. ELMSLY, J. CAMPBELL, in the Strand; and T. DAVIES, in Ruffel-Street, Covent-Garden.
M.DCC.LXX.

drew upon his *own* early herbals for text figures when writing his later ones. Hill's position as a systematic botanist is attested by Jacquin naming in his honor a genus, *Hillia,* and by the number of species in our flora to-day which are credited to him, from the establishment of the year 1753 as the base line for plant nomenclature. The King of Sweden recognized the value of the "Vegetable System" by granting its author the Order of Vasa,

and thereafter Hill employed the title, Sir. He was also elected a member of the Imperial Academy and a fellow of the Royal Academy of Sciences at Bordeaux.

Systematic botany was in vogue when Hill was writing, so it is not strange that he devoted himself largely to this aspect of the science, but it is rather remarkable that he undertook some interesting studies in plant anatomy since, during the eighteenth century, little had been added to the basic work of Malpighi and Grew.

Hill's investigations in this field are included in a volume entitled "The Construction of Timber, from its Early Growth; Explained by the Microscope and proved from Experiments in a Great Variety of Kinds." This was published in 1770 and a new edition appeared four years later with an additional chapter on "the strange disposition of the vessels in the ferns." The work shows that Hill possessed unusual technical ability with a newly invented instrument for section cutting, the forerunner of the modern microtome, and with his own improved compound microscope. After describing these devices, the author proceeds to a general account of tissues and their distribution in plant stems, taking up his observations under five chief headings: "the constituent parts of timber; the vessels of trees; the encrease by growth; the different disposition of the parts in various trees"; and "the particularities in the vessels of trees." The critical comparison of the tissues in various plants is well illustrated with copper plates which represent sections not very highly magnified, but nevertheless bear favorable comparison with many in the works of Grew and Malpighi. Hill's incursion into plant histology, prompted by a life-long interest in studies with the microscope, foreshadows the intensive work by other investigators as the century closed. Hill, however, left the subject almost where he found it.

As early as 1757 Hill became interested in the physiology of plants and published a pamphlet, already mentioned, entitled "The Sleep of Plants and Causes of Mo-

tion in the Sensitive Plant Explain'd,'' in the form of a letter addressed to Linnaeus, who had referred to the phenomenon in question as ''sleep.'' The same year the observations were incorporated in his large volume, ''Eden, or a Compleat Body of Gardening.''[21]

A critical study of the monograph shows clearly that Hill possessed unusual aptitude for the analysis of physiological phenomena by the experimental method, a talent by no means commonly exhibited at the time, although Hales's ''Vegetable Staticks'' had shown the way. For example, Hill emphasizes the necessity of studying separately the various physical factors of the plant's environment and then combining them in the ways they normally act upon the organism; the importance of keeping all the conditions, except the one purposely varied, absolutely constant during experimentation, and, finally, the value of comparing the results from experiments on different species of plants. Thus, in studying the response to light of *Mimosa* and *Abrus,* he found that ''in these and in all others, the degree of elevation or expansion in the lobes is exactly proportional to the quality of the light: and is solely dependent upon it.'' Hill, of course, made mistakes in his observations and interpretations, but taken as a whole this brief study is a neatly executed and most interesting contribution, antedating by a year Du Hamel's well-known ''Physique des arbres.''

Turning from the ''Sleep of Plants,'' Hill found time to publish in 1758 a monograph entitled ''Outlines of a System of Vegetable Generation,'' in which he endeavored to show that the pollen grain contains an embryo which it sets free when deposited on the stigma. Obviously, he saw the contents of the pollen grain and misinterpreted it as an embryo. He noted that pollen grains burst when placed in a drop of water and concluded that a similar bursting and setting free of the embryo took place on the wet stigma, a phenomenon rediscovered 138 years later by Lindforss.

[21] Pp. 703–708.

E D E N:

OR, A

COMPLEAT BODY

OF

GARDENING.

CONTAINING

PLAIN and FAMILIAR DIRECTIONS

FOR

Raising the several useful PRODUCTS of a GARDEN,

FRUITS, ROOTS, and HERBAGE;

From the PRACTICE of the most successful GARDENERS,

AND

The RESULT of a LONG EXPERIENCE.

TOGETHER WITH

The Culture of all Kinds of FLOWERS, according to the Methods of the ENGLISH FRENCH, and DUTCH FLORISTS.

AND

The Knowledge of Curious PLANTS, after the System of LINNÆUS.

WITH

FIGURES and DESCRIPTIONS of the FLOWERS and PLANTS proper for a Garden,

INCLUDING

The CARE and CULTURE of the PLEASURE-GARDEN.

The BUSINESS of the SEMINARY for every Week in the Year.

CATALOGUES and accurate DESCRIPTIONS of the FRUITS as they come into Season;

AND

New and PRACTICAL DIRECTIONS for the Management of FRUIT-TREES.

With the best Methods of Culture for

The several ARTICLES of the KITCHEN-GARDEN:

AND THE

Compleat Management of the Ground for raising them, in the NATURAL and ARTIFICIAL Manner.

Compiled and Digested from the PAPERS of the late celebrated Mr. HALE,

By the AUTHORS of the COMPLEAT BODY of HUSBANDRY.

And comprehending

The ART of constructing a GARDEN for USE and PLEASURE;

The best METHODS of keeping it in ORDER:

AND

The most perfect ACCOUNTS of its several PRODUCTS.

LONDON:

Printed for T. OSBORNE, in Gray's Inn; T. TRYE, near Gray's Inn Gate, Holborn, S. CROWDER and Co. on London Bridge; and H. WOODGATE, at the Golden Ball in Pater-noster-Row.

MDCCLVII.

Even a brief survey of the "Proteus Hill," the "Cain of Literature," the "quack and blustering adventurer," the "Halloway of his day," the man with "cowardice that seemed a disease"—to borrow epithets from biographers of his enemies—would be incomplete without at

least mentioning by title a few other samples of his prodigious literary output: "A History of the Materia Medica" (1751), "Adventures of Mr. George Edwards, a Creole" (1751); "The Story of Elizabeth Canning Considered. With remarks on what has been called A Clear State of her Case, by Mr. Fielding" (1753); "Observations on the Greek and Roman Classics: Series of Letters to a Young Nobleman, now published for the Use of Gentlemen at the University" (1753); "Urania, or a Compleat View of the Heavens; Containing the Ancient and Modern Astronomy in Form of a Dictionary" (1754); "Thoughts Concerning God and Nature, in Answer to Lord Bolingbroke's Philosophy" (1755); "The Maiden's Whim, or the Critical Minute"—a play (1756); "The Naval History of Britain" (1756); "Compleat Body of Husbandry" (1756); and "The Management of the Gout, with the Virtues of Burdock Root" (1758).

Such are some other titles which attract our attention during merely the first decade of his career. Much, to be sure, is hack work, but most of it is exceedingly well done. His "Husbandry" and "Gardening" are among the first works in which scientific knowledge was put in a popular form by being issued in weekly installments. He was still "going strong" to the day of his death, writing pamphlets on the virtues of sage, polypody, bardana and the rest which enjoyed a wide sale and gave him a living, while he was struggling to publish the last volumes of the "Vegetable System." That he believed in the efficacy of the herbs he exploited there is little reason to doubt. More than once he expressed his view that the modern "chemical medicines" were dangerous, especially when not specifically prescribed by a physician. Perhaps a great deal can be read between these lines from his "Virtues of British Herbs": "He who seeks the herb for the cure, will find it half effected by the walk." This aspect of the doctor was crystallized in many a literary compliment:

Thou essence of dock, valerian and sage,
At once the disgrace and the pest of the age;
The worst we can wish you for all your dam'd crimes
Is to take thy own physics and read thy own rhymes.[22]

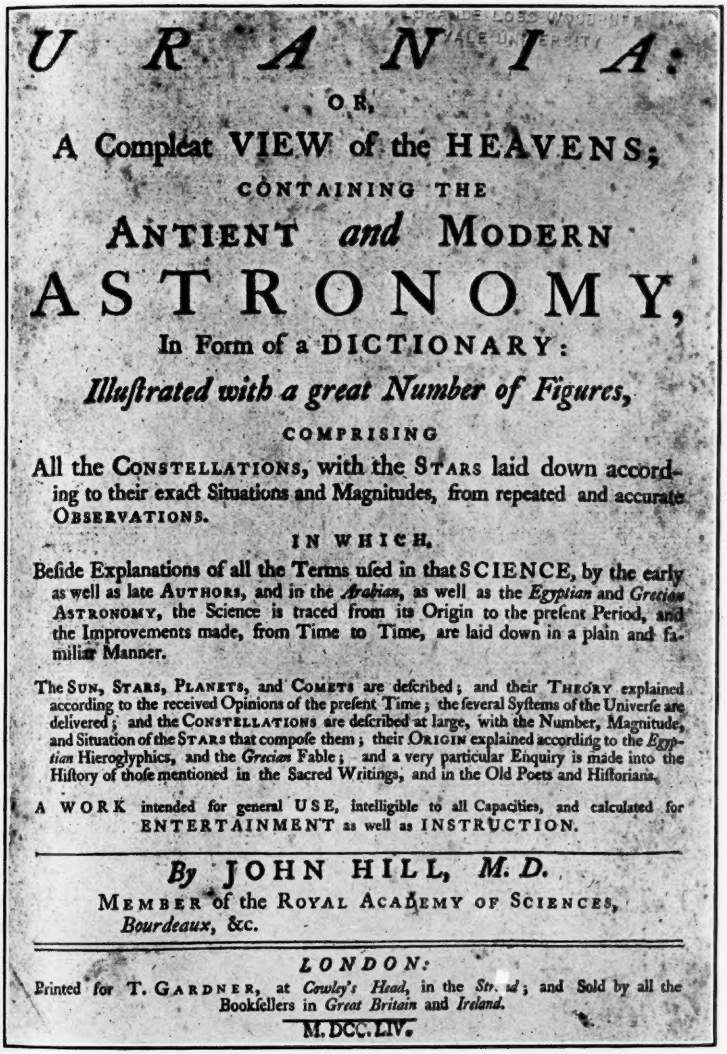
And, as if this were not enough, the famous "Mrs. Glasse's Cookery" was attributed to Hill. Surely we must credit him with moral courage in enduring "with undiminished spirit the most biting satires, the most wounding epigrams, and most palpable castigations." To Smart's "Hilliad," which called him "Th' insolvent tenant of encumber'd space," he flung a "Smartiad";[23] and to the charge of unbounded conceit and effrontery, he replied, "No one knows more the narrow limits of human knowledge; or entertains an humbler opinion of the returns of years of application."

Still another facet of Hill's many-sided personality is revealed by his stout volume, "Thoughts Concerning God and Nature, in Answer to Lord Bolingbroke's Philosophy," which reveals a breadth of view and familiarity with a field of literature which might not be expected of the doctor. The volume was apparently published at some expense to the author, since he says that if the entire edition were sold, it would not cover the cost of printing. The book is in no sense a stereotyped "natural theology" after the fashion of the time, though he justly states: "It is certain that God is to be perceived by the most slight view of the universe; and it is as certain, that the more precise and accurate that view is made, the more plainly, the more fully and the more distinctly that God is seen. This is the last affirmation of all true wisdom."

A summary view of Dr. John Hill—indeed, any view must be a summary—though from the vantage point of

[22] *Cf.* Percy Fitzgerald, "Life of David Garrick," Rev. Ed., 1899.

[23] Christopher Smart, "The Hilliad," London, 1753. Republished in Reed's Repository, London, 1783. John Hill, "The Smartiad," London, 1753.



URANIA:

OR,

A Compleat VIEW of the HEAVENS;

CONTAINING THE

ANTIENT *and* MODERN

ASTRONOMY,

In Form of a DICTIONARY:

Illustrated with a great Number of Figures,

COMPRISING

All the CONSTELLATIONS, with the STARS laid down according to their exact Situations and Magnitudes, from repeated and accurate OBSERVATIONS.

IN WHICH,

Beside Explanations of all the Terms used in that SCIENCE, by the early as well as late AUTHORS, and in the *Arabian*, as well as the *Egyptian* and *Grecian* ASTRONOMY, the Science is traced from its Origin to the present Period, and the Improvements made, from Time to Time, are laid down in a plain and familiar Manner.

The SUN, STARS, PLANETS, and COMETS are described; and their THEORY explained according to the received Opinions of the present Time; the several Systems of the Universe are delivered; and the CONSTELLATIONS are described at large, with the Number, Magnitude, and Situation of the STARS that compose them; their ORIGIN explained according to the *Egyptian* Hieroglyphics, and the *Grecian* Fable; and a very particular Enquiry is made into the History of those mentioned in the Sacred Writings, and in the Old Poets and Historians.

A WORK intended for general USE, intelligible to all Capacities, and calculated for ENTERTAINMENT as well as INSTRUCTION.

By JOHN HILL, *M.D.*

MEMBER of the ROYAL ACADEMY OF SCIENCES, *Bourdeaux*, &c.

LONDON:

Printed for T. GARDNER, at *Cowley's Head*, in the *Strand*; and Sold by all the Booksellers in *Great Britain* and *Ireland*.

M.DCC.LIV.

nearly two elapsed centuries, does neither Hill nor his enemies justice. So much, however, is clear: Hill was endowed with remarkable talents which warranted his holding a commanding position among scientific men, but he largely dissipated this birthright by a temperament which made himself his own worst enemy. A contemporary, who was not a friend, said the doctor was "of all men I ever knew so mixed a character, none but himself can be his parallel." And this estimate can not be improved to-day.

TWO WING MUTATIONS IN HABROBRACON AND THEIR METHOD OF INHERITANCE

DR. P. W. WHITING
UNIVERSITY OF MAINE

Introduction

In previous papers on genetics of the parasitic wasp, *Habrobracon juglandis* (Ashmead), heredity of factors affecting eye color and of factors causing defects in vein r_4 has been discussed.

A series of quadruple allelomorphs—typical jet black, light ocelli, orange and ivory has been shown (Whiting, Anna R., and Burton, Raymond H., 1926). These, which have been associated with certain minor factors for defective venation and with a lethal, may be regarded as located in Chromosome I (Whiting, P. W., 1926).

A factor for defective venation ($d_{II\,95}$) causing about 95 per cent. of males and 90 per cent. of females in pure stock to show defective venation is apparently independent of orange and its allelomorphs. It shows linkage with the main factor for sooty mesosternum (s_{II}). These may be regarded as located in Chromosome II (Whiting, P. W., 1926).

Numerous other factors for defective and for sooty of differing potencies occur.

Heredity is sex-linkoid; females are of biparental origin; males, with the expection of the few anomalous or patroclinous males from fertilized eggs, are from reduced unfertilized eggs and therefore occur in gametic ratios.

Presentation of Data

WRINKLED WINGS (w)

Origin

A certain inbred line which contained the factors for orange eyes (o) and for defective r_4 veins ($d_{II\,95}$) may be

traced back to Lancaster stocks 6 and 10 and Iowa City stock 11. Females were isolated after having mated with their brothers.

After thirteen generations consisting in all of 1,150 males and 521 females, none of which showed any wrinkled wings, although an occasional wrinkled appeared in branch lines, a certain fraternity (995) was produced consisting of thirty-three males and twenty-eight females, also with flat wings. After having been with their brothers, ten of these females were isolated. Nine produced 329 males and seventy-eight females; three of these, one male and two females, had wings wrinkled or deformed. The tenth isolated female produced six flat-winged males, seven wrinkled-winged males, and four flat-winged females. This fraternity (1007.4) forms the basis of the wrinkled-winged stock. The three wrinkled occurring in the cousins are not to be thought of as genetically comparable with "wrinkled" (w) as other factors of complicated nature occurred in the fraternities causing occasional malformation of wings. Moreover, each of the three occurred in a different fraternity and two were females. The chances of a female displaying the recessive mutant character are very unlikely, since she must have received the factor w from both parents.

Since the fraternity showing wrinkled displayed the character in the males it is to be supposed that the mother carried the factor. The mutation may have occurred in her own development or else was present in the sperm or egg producing her. It could not have been present in any large proportion of her mother's eggs, for none of her thirty-three brothers showed the character; nor is it likely to have been present in any very large proportion of her father's sperm, since none of her nine sisters tested transmitted it.

Description of Character

The character wrinkled appears to be due to difficulty in disposing of the delicate pupal membrane as the wasp

matures. Ordinarily this breaks and is cast off before the wings expand. In wrinkled wasps wing expansion is interfered with especially and often the pupae die before eclosion. Occasionally normal development of the legs may be prevented and frequently antennae have shreds of this membrane adhering or several joints may be enclosed. Terminal joints may be broken off, perhaps as a result of attempts to remove the membrane. In the more normal individuals antennae are clean but one or both wings may be more or less shrivelled or slightly wrinkled especially toward the tip. No detailed study of the development or causes of failure to shed the membrane has been made.

Heredity

Relation to type:

Three females were isolated from culture 1007.4. Two produced fifty-eight flat males and four flat females. The third produced four flat males, four wrinkled males and ten flat females. In subsequent generations wrinkled males were used wherever possible. Heterozygous females produced males, 340 flat and 301 wrinkled. When they were mated with wrinkled males their daughters were twenty-seven flat and twenty-two wrinkled. Wrinkled females by wrinkled males produced flat males two, wrinkled males sixty, wrinkled females two. The difficulty in maintaining the stock in pure condition on account of low viability, especially in the females, made it advisable to discontinue the line. The factor was preserved by crossing with other stocks. In later generations wrinkled females heterozygous for orange, produced males—type five, wrinkled 138, orange seven, orange wrinkled 129. Males from wrinkled females were therefore fourteen flat to 327 wrinkled or 95.9 per cent. wrinkled. This indicates that wrinkled overlaps with normal to some extent.

That wrinkled is recessive or nearly so is shown by crosses of wrinkled males to females homozygous for

flat wings. Such crosses with females of stocks 1, 9, 10, 11, 17, and miscellaneous females yielded flat males 886, flat females 782 and wrinkled females four. It is altogether possible that the factor w may have been effective in determining the character of the four wrinkled females. Since wrinkled may appear occasionally, however, without the presence of w it can not be stated that there is any irregularity of dominance here.

Relation to locus for orange eye:

F_2 males from crosses involving wrinkled and orange or its allelomorphs indicate no significant linkage.

From type females from various sources by orange wrinkled males F_2 males were type 889, orange 767, wrinkled 675, and orange wrinkled 738; 1,442 or 46.986 $\pm$ 0.608 per cent. recombinations out of 3,069.

From orange by wrinkled from various sources F_2 males were type 629, orange 717, wrinkled 596, and orange wrinkled 605; 1,234 or 48.449 $\pm$ 0.668 per cent. recombinations out of 2,547.

From seven virgin orange females from ivory by orange wrinkled there were produced 522 males—orange 128, orange wrinkled 134, ivory 130 and ivory wrinkled 130; 258 or 49.425 $\pm$ 1.476 per cent. recombinations.

Total recombinations among the 6,138 F_2 males are 2,934 or 47.801 $\pm$ 0.430 per cent.

Since the above ratios show a barely significant difference from the fifty per cent. expected on free recombination, wrinkled can not at present be included in Chromosome I. The somatic overlapping of wrinkled with normal would tend to decrease apparent linkage if such exists.

Relation to main factor for defective r_4 vein ($d_{II\ 95}$):

The character of vein r_4 can not be conveniently identified in the majority of wasps with wrinkled wings. Crosses of wrinkled by defective from various sources were made. It is certain that the defective had $d_{II\ 95}$, but highly probable that they had also minor factors for defective as well. F_2 males were type 255, defective 303,

and wrinkled, including wrinkled defective, 466. Among the 558 flat-winged wasps the 255 or 45.699 ± 1.422 per cent. with normal venation indicate recombination, except that a small percentage of these may be somatic overlaps from defective. On the other hand, an unknown but small proportion of the 303 defective may be lacking in $d_{II\,95}$ but possess minor factors for defective. The figures therefore indicate only that if linkage exists it is not very close.

A cross was made between a wrinkled male from stock 22 and a defective female from stock 10. These stocks are related since they were derived by breeding up to the same stock, type stock 1. From eighteen virgin F_1 females were reared 1,847 males—type 481, defective 510, wrinkled normal 161, and wrinkled defective 133, besides 562 wrinkled in which venation character could not be distinguished. There are 856 or 46.345 ± 0.782 per cent. wrinkled, of which only 294 or 34.346 ± 1.095 per cent. had wings sufficiently flat to determine venation character. In case a defect was noted in r_4 of one wing the wasp was recorded as defective, even though the other wing was much wrinkled. Normal venation was certain only in case r_4 could be observed in both wings. This would tend to increase the wrinkled group in which condition of r_4 was uncertain, at the expense of wrinkled normal more than of wrinkled defective. Nevertheless, wrinkled normal, a parental class, exceeds the recombination group wrinkled defective. Among the flat-winged the parental class, defective, exceeds the normal type group. Disregarding those in which venation character could not be distinguished, out of the total of 1,285 there are 614 or 47.782 ± 0.940 per cent. recombinations. This can not be considered as significantly different from expectation on a basis of free assortment.

REDUCED WINGS (R)

Origin

In March, 1925, Miss Achsa Bean, a student at the University of Maine, found in the F_2 generation from a

stock 8 (orange-eyed Lancaster) female by a stock 11 (black-eyed Iowa City) male a small black-eyed male with wings that were much reduced in size and venation. This mutant (Freak 268) was mated to a female from type stock 1. Reduced appeared among the F_2 males.

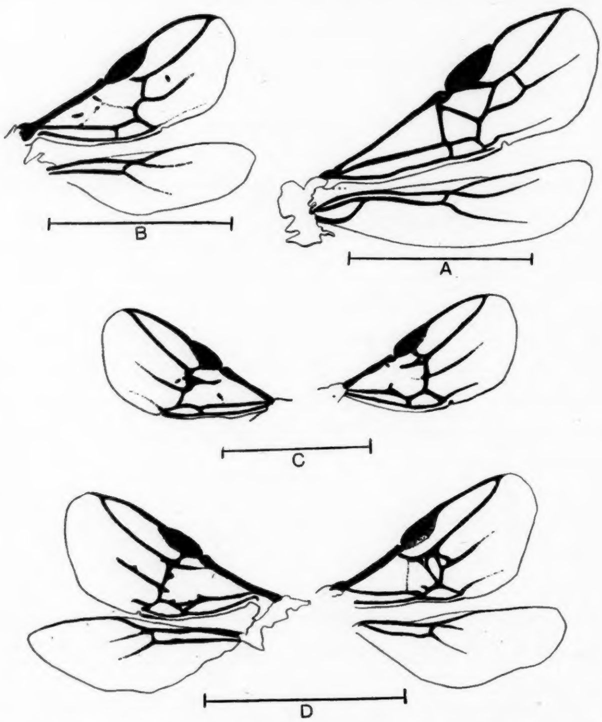


FIG. 1. A. Right wings of normal female. B.–D. Wings of reduced females. Beneath each set of wings is shown comparative length of abdomen from base to tip. ×20.

Description of Character

The character of reduced is shown in Fig. 1, B–D. Fig. 1A shows normal wings for comparison. All figures are drawn from females. They are magnified twenty diameters. The horizontal line below each set of wings repre-

sents the length of the abdomen from base to tip, not including the sting. It may be seen that primary wings are most affected, although the secondaries are reduced somewhat in length and venation. Very great variability obtains in the venation of the primaries so that no two wings appear to be similar. General body size is not appreciably affected, as may be noted from abdominal length in Fig. 1, B and D. C shows the venation of the primaries of a small specimen.

It appears that vein r_4 is usually lacking, although occasionally it is complete. Traces of it may be seen in Fig. 1 B and in the left wing of D.

Heredity

Relation to type:

Reduced males were crossed with orange females (stock 8). There were produced thirty black-eyed patroclinous males, of which twenty-two had wings of normal size with r_4 complete, five had wings of normal size with r_4 defective, one had wrinkled wings and two died as naked pupae, no cocoons being present. There were 758 orange-eyed males, of which one died as a naked pupa. The other 757 had normal wings with normal venation, but one had deficient genitalia and digestive tract. Among the 808 black-eyed daughters, fifteen had defective r_4, one had abdominal sclerites disarranged, one had deficient digestive tract and one deformed gonapophyses.

The occurrence of defects in r_4 among the black-eyed males and females and its normality among all the orange-eyed males indicates paternal inheritance of minor factors for defective since $d_{II\ 95}$ was not present. Full size of wings in the black-eyed males indicates maternal inheritance. They are presumably diploid (Whiting, P. W., and Whiting, Anna R. 1925). The occurrence of a greater ratio of freaks and naked pupae among the patroclinous males than among their sibs and of a greater ratio of freaks among the females than among

their normal brothers is in line with the findings of Anna R. Whiting (1925, pp. 41 and 42).

Reduced males were also crossed to ivory defective females (stock 17). Besides the 119 regular ivory males, eight normal and 111 defective, and the 110 black-eyed females, forty-four normal and sixty-six defective, were three black-eyed patroclinous males, one dying as a naked pupa, the other two maturing with full-sized wings with defective r_4.

Miscellaneous crosses of normal females by reduced males yielded 548 males and 253 females, all with full-sized wings. The crosses of females from stock 8, stock 17, and miscellaneous by reduced males, recorded above, have therefore yielded 1,171 females with wings of approximately normal size and showing none of the disarrangement and reduction of veins characteristic of reduced. The character is therefore recessive.

Reduced females were obtained by crossing reduced males to heterozygous females. Such crosses yielded type males 170, reduced males 179, type females 162, and reduced females 176.

Reduced has consistently bred true when isolated in stock.

Ivory wrinkled males were crossed to orange reduced females. Progeny were all orange, twenty-one males and seventy females. Seventeen males were reduced. The females and four of the males had full-sized flat wings. Among these males, patroclinous with respect to size of wings, was one with genitalia deficient. These irregular males, like their sisters, showed the dominant allelomorph to reduced inherited from their fathers and the dominant allelomorph to wrinkled inherited from their mothers.

Black-eyed wrinkled males were crossed to orange reduced females. Among the seventy-nine males resulting were sixty-nine orange reduced, nine black-eyed with normal-sized flat wings and one black-eyed naked pupa. The 109 black-eyed females had full-sized flat wings as

expected. The patroclinous males like their sisters show dominant traits of paternal and maternal origin and are presumably diploid.

Relation to locus for orange eye:

The F_2 males from reduced males by orange females (stock 8) were type 177, orange 166, reduced 195 (ten having r_4 complete in both wings) and orange reduced 202 (seven having r_4 complete in both wings). F_2 females were type fifty-nine and orange eighty-four. Out of the total of 740 males there are 379 or 51.216 ± 1.240 per cent. recombinations.

Orange reduced males were crossed to type females (stock 1). F_2 consisted of males—type twenty-seven, orange nineteen, reduced fifteen, and orange reduced twenty-one, and type females 147.

F_2 from orange reduced females by wrinkled males consisted of males—type sixty-two, orange fifty-five, wrinkled thirty-two, reduced fifty-four, orange wrinkled thirty-nine, orange reduced sixty, wrinkled reduced twenty-one, and orange wrinkled reduced thirty-seven.

With respect to reduced and orange we have therefore from type by orange reduced, 444 males—type 121, orange 113, reduced ninety-two, and orange reduced 118; 205 or 46.171 ± 1.596 per cent. recombinations.

F_2 from ivory defective females (stock 17) by reduced males consisted of 1,221 males—type 159, ivory 176, defective 133, reduced twenty-six, ivory defective 127, ivory reduced sixteen, defective reduced 286, ivory defective reduced 298, and 217 females—type fifty-four, defective fifty-two, ivory fifty-eight, and ivory defective fifty-three.

If the males be summarized with respect to ivory and reduced alone there are type 292, ivory 303, reduced 312, and ivory reduced 314; 606 or 49.631 ± 0.965 per cent. recombinations out of 1,221, indicating no linkage between reduced and ivory.

F_2 from orange reduced females by ivory wrinkled males consisted of 421 males—orange forty-nine, ivory sixty-one, orange wrinkled thirty-seven, orange reduced

sixty-one, ivory wrinkled thirty-four, ivory reduced sixty, orange wrinkled reduced sixty-six, ivory wrinkled reduced fifty-three, and 130 females—orange sixty-six, orange wrinkled three, orange reduced sixty, orange wrinkled reduced one. The wrinkled females may be due to irregularity in dominance of W over w or to other factors.

If the males be summarized with respect to ivory and reduced there are orange eighty-six, ivory ninety-five, orange reduced 127, and ivory reduced 113; 199 or 47.268 ± 1.641 per cent. recombinations out of 421.

Out of a grand total of 2,826 F_2 involving orange or its allelomorphs and reduced there are 1,389 or 49.151 ± 0.634 per cent. recombinations. There is therefore no linkage between reduced and the locus for orange.

Relation to factors for defective r_r vein:

Among the 397 F_2 reduced males from orange females (stock 8) by reduced males were only seventeen or 4.282 ± 0.685 per cent. with r_4 complete, although factors for defective r_4 affecting the full-sized wing were not present.

Among the 626 F_2 reduced males from ivory defective females (stock 17) by reduced males were forty-two or 6.709 ± 0.674 per cent. with r_4 complete. Although factors for defective r_4 including the very potent $d_{II\ 95}$ were present here, the ratio of reduced with r_4 normal is actually higher than in F_2 from reduced by stock 8. The difference in percentage, 2.427 ± 0.961, is not significant. It may be concluded that factors for defective r_4 affecting full-sized wings have little if any effect upon reduced.

If the F_2 males from ivory defective females (stock 17) by reduced males be summarized with respect to reduced and defective alone there are type 335, defective 260, reduced forty-two, and defective reduced 584. Only wasps with full-sized wings are of value for testing linkage because of the obscuring effect of reduced. Among the 595 of these, 335 or 56.302 ± 1.371 per cent. represent the class not occurring in the parents. There are significantly more apparent crossovers than would be expected

on a basis of no linkage. Since defective overlaps with normal this discrepancy may be readily explained. The figures indicate no linkage between reduced and defective $d_{II\ 95}$.

Relation Between Wrinkled (*w*) *and Reduced* (*r*)

If the 421 F_2 males from orange reduced females by ivory wrinkled males be summarized with respect to wrinkled and reduced alone, there are type 110, wrinkled seventy-one, reduced 121, and wrinkled reduced 119.

If the 360 F_2 males from orange reduced females by wrinkled males be similarly summarized there are type 117, wrinkled seventy-one, reduced 114, and wrinkled reduced fifty-eight.

112 F_2 males from wrinkled by reduced from miscellaneous sources are type thirty-four, wrinkled twenty-six, reduced twenty-five, and wrinkled reduced twenty-seven.

Certain errors may occur in counts involving wrinkled in combination with reduced besides the overlap of wrinkied to normal. Extreme wrinkled may at times be taken for wrinkled reduced. Moreover, all wrinkled or wrinkled reduced may not be counted, as they may die in the cocoons. Significant departures from expectation in the above counts may be due to one or more of these causes, which must to some extent affect apparent ratios of recombinations.

The grand total of 893 F_2 males from wrinkled by reduced consisted of type 261, wrinkled 168, reduced 260, and wrinkled reduced 204; 465 or 52.717 ± 1.127 per cent. recombinations, indicating free assortment between wrinkled and reduced.

Summary

The origin and genetic relationships of two mutations in the parasitic wasp, *Habrobracon juglandis* (Ashmead) are given.

Wrinkled wings (w) appear to be due to inability to shed the pupal membrane. Expansion of the wings is

hindered. The character overlaps somewhat with type.

Reduced (r) causes the wings, especially the primaries, to be much shortened and the veins to be reduced or fused together. The character does not overlap with type. Vein r_4 is lacking in the great majority of reduced, whether factors for defective r_4 are present or absent.

Both mutations are recessive or nearly so. Their method of inheritance is sex-linkoid. In crosses with type "patroclinous" males display the dominant trait as do their sisters. The cross of wrinkled with reduced reconstitutes the double dominant flat full-sized wing, both in daughters and in patroclinous sons.

Wrinkled and reduced are independently inherited and show no linkage with the orange eye locus (Chromosome I), nor with the main factor causing defect in vein r_4 ($d_{II\ 95}$ of Chromosome II).

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1860—1894—1926[1]

PROFESSOR F. O. BOWER, ScD., D.Sc., LL.D., F.R.S.

The future of Biology lies not in generalization but in closer and closer analysis.—BATESON (Birkbeck Lecture, 1924).

DEATH sudden and wholly unforeseen has stepped between this section and the president of its choice. Professor Bateson had presided over the whole association at its meeting in Australia, and partly on that account he had been specially selected for the chair of this section in Oxford. From him we might have expected a broad outlook upon biological science. His address would have been instinct with wide experience in both of the branches of living things, the interests of which interweave in enthralling and often most perplexing ways. We should have heard a fearless statement of his mature views. Something constructive would certainly have justified the congratulations with which some of us had already welcomed his nomination. A great figure has been taken from the arena of biological science. A career still full of the promise of further achievement has closed prematurely.

This is not the time or the place for any comprehensive obituary of Bateson; nor would I divert your attention from those already before you, written by more competent hands. I will only allude briefly to four leading events in his scientific career. He felt in early life the lack of facts bearing on variation, and sought to extend their area in his great work "Materials for the Study of Variation," published in 1894. This was the year when the association last met in Oxford. I do not remember that its contents came into the discussions in Section D, though the book centered upon the vital question of continuity and discontinuity. The second event was the

[1] Address of the president of Section K—Botany—British Association for the Advancement of Science, Oxford, August, 1926.

publication in 1902 of "Mendel's Principles of Heredity," in which, though essentially a controversial statement, Bateson perceived latent in the rediscovered writings an expanding vista of advance. "Each conception of life," he says, "in which heredity bears a part must change before the coming rush of facts." In a third stage of his work Bateson expanded this theme into a fuller statement under the same title, and it was published in 1909. Passing from this period of high hopes to the fourth phase of 1924, we see in his address at the Birkbeck Centenary a chastened attitude. He there remarks: "We must frankly admit that modern discoveries have given little aid with the problem of adaptation," and that, much as Mendelian analysis has done, "it has not given us the origin of species." But that analysis having "led to the discovery of transferable characters, we now know upon what to concentrate. . . . Henceforth the study of evolution is in the hands of the cytologist acting in conjunction with the experimental breeder. Every appeal," he says, "must ultimately be to the mechanics of cell-division. The cell is a vortex of chemical and molecular change. . . . The study of these vortices is biology, and the place at which we must look for our answer is cell-division." I would ask you to mark that last word. It is cell-division, not nuclear division; and earlier in his address we find the pregnant sentences: "As to what the rest of the cell is doing, apart from the chromosomes, we know little. Perhaps the true specific characters belong to the cytoplasm, but these are only idle speculations." Such extracts from Bateson's latest public pronouncement may suggest to you what the section has lost by his death. They show the mind still elastic and perceptive: still both constructive and critical.

Any address that follows such a tragedy of disappointment as the section has suffered can only fall short of what we had hoped to hear. Instead of attempting to fill the broad biological rôle that naturally fell to Bateson, I propose to center my remarks upon three dates

when the association has met in Oxford, *viz.*, 1860, 1894 and 1926. It happens that these dates mark approximately periods of transition in the progress of biological science, and particularly in botany.

1860

I need not remind you of the fact that the meeting in Oxford of 1860, the year after the publication of the "Origin of Species," witnessed the clash between the new view and the opposition it was certain to arouse. The story has been often told of the aggressive attack and the crushing retort. But it is not sufficiently recognized that, though Huxley bore the first brunt of the fight, a large part in the contest was taken by Hooker. The meeting closed after he had spoken, and in his own words he was "congratulated and thanked by the blackest coats and the whitest stocks in Oxford."

Two generations have passed since the Oxford meeting of 1860: and still the "Origin of Species" holds its place as a great philosophical pronouncement. As the methods of research passed into greater detail, the area of fact has been extended through the labors of an ever-growing army of inquirers, and naturally divergences of view have arisen. Some authors appear to demand that for all time the "Origin" must cover every new aspect of biological inquiry, or else the whole theory crumbles. That is to demand a prophetic vision for its author. We need not for the moment follow these or other criticisms, but rather recognize that the theory rested essentially on facts of heritable variation, without defining their magnitude, limitations or origin; and that it explained a means of their summation so as to produce progressive morphological results. As an index of current opinion on the validity of Darwin's theory as a whole, I would draw your attention to three British works on evolution, all published within the last two years. In 1924 Dr. Scott concludes his volume on "Extinct Plants and Problems of Evolution" with the judicious sentence: "I may ven-

ture . . . to maintain that a consideration of all the evidence . . . is on the whole favorable to the old, truly Darwinian conception of an orderly and gradual evolution without sudden and inexplicable leaps, an evolution in harmony with the uniformitarian principles established by Lyell." But he remarks that he does not favor any exaggerated ideas such as the so-called "omnipotence of natural selection."

In the present year Professor Graham Kerr, in his volume on "Evolution," also adopts a distinctly Darwinian position, but with greater stress laid upon the potency of natural selection; this might be expected from one who spent some of his most impressionable years in the wild surroundings of the Gran Chaco. He speaks from experience of the effect of selection as being "in actual fact enormous," and he holds that the attempts that have been made to minimize its importance are to a great extent fallacious. He sees in the recognition of Mendelian inheritance that the natural selection theory has been greatly fortified since Darwin's day. Variability, upon which the theory depends, he regards as an expression of that instability which constitutes one of the inherent and most characteristic features of living substance, and he states that such variation has to be accepted as a basic fact. He further regards as an added strength to the Darwinian theory "the recognition that a particular variation is the outward expression of a *tendency* to vary in that particular direction, and that as a consequence the selection of variations in a particular direction involves a necessary intensifying of the tendency towards that particular variation, and in turn the encouragement of evolutionary progress along a definite directed line." These expressions are in general accord with the doctrine of Weismann that acquired characters, or, as Graham Kerr terms them "impressed" characters, are not themselves inherited. It is not for a botanist to interfere with the arguments of zoologists on this question, as applied in their own science. There are,

however, zoologists who strongly maintain their belief in such inheritance, a position upheld by Professor MacBride in the volume on "Evolution" published last year by Messrs. Blackie, which is the third of the works above mentioned.

In that same volume I took the opportunity of stating that the question of the origin of heritable characters, or mutations as they are called, is still quite an open one for plants. But it was maintained that a wide latitude of time is a real factor in the problem. This was already recognized by Hofmeister, who on the last page of his "Allgemeine Morphologie" said: "It appears to me probable that only gradually, in the course of many years' development, the influential effects on outer form appeared and became hereditary." Thus Hofmeister contemplated a slow inheritance of acquired or impressed characters in plants. To any one who notes how directly susceptible individual plants are to external conditions, and how greatly these affect their individual form, it would seem improbable that there should be any sharp line of demarcation between the individual and the racial life, or that what affects every individual plant so profoundly should never affect the race. In my essay in Messrs. Blackie's volume on "Evolution" I advanced comparative evidence, which commends itself to my own mind as a morphologist, indicating that the boundary between fluctuating variations and heritable mutations is not absolute: in fact, that in plants, given latitude of time, variations related causally with external circumstance, and not merely initiated at random, are liable to be transmitted to the offspring. There is no need to repeat the argument here, for it was submitted to the section at Southampton. It may be remarked that this is in direct opposition to the doctrine which Weismann laid down with special reference to the animal kingdom. But what may be applicable for one kingdom of living things does not necessarily apply for the other. The evolution of animals and plants has certainly been homo-

plastic in all its later stages. Our minds should be perfectly free to follow the facts of our own science to their legitimate conclusions. These indicate to me that heritable variations in plants have been promoted or actually determined in their direction or their number or their quality in some way by external conditions. But these need not necessarily have worked within restricted time-limits of present experiment; for the wide latitude of geological time has been available for evolution to proceed. Hence negative results of the experiments of a few years need not be held as overruling the conclusions drawn from comparison of nearly allied forms.[2]

Before we leave this historical aspect of evolution a moral may be drawn from the lives of its four protagonists of 1860. Darwin, Wallace, Hooker and Huxley were all equipped for the battle from the armory of personal experience in the great world. The theory of evolution was born and bred of foreign travel, and upon foreign travel quite as much as upon quiet work at home its future still depends. We should not for a moment minimize the great developments of laboratory study and of breeding experiment in recent years that bear upon its progress. But it is not thence alone that the fullest achievement can be anticipated. The cytologist and the breeder, just as much as the abstract theorist, should know nature face to face, not merely through a glass darkly. To those who believe in the close relation between environment and variation, which is to me the very core of evolution, this seems essential to any well-balanced view. The open forest, the sea-coast, steppe and mountain-side should be regarded as the natural complement to the laboratory and the breeding-station. No one, morphologist or physiologist, should hold himself equipped for research or fully qualified to teach un-

[2] Gates, in his volume on the "Mutation Factor in Evolution" (1915), draws to a close with words that may well be quoted here. "It would appear," he says, "that something within the organism is responsible for such unswerving progress in a given direction as appears to be repeated over and over again in the paleontological record."

less he have at least some experience of travel through wild nature. This can best be acquired in the tropics. But what do we find?

In 1886 a committee of this association was appointed to assist the visits of botanists to Ceylon for study. Several well-known botanists availed themselves of its aid; but after a few years the scheme flickered out through inanition. In 1909 I visited the Cinchona Station in Jamaica, and again a scheme for continued use of the station by British botanists was initiated; but it has since died out for want of consistent support. Why did these efforts fail? We may set these failures down to undervaluation of the importance of foreign, and particularly of tropical, study; and the lack of full perception that open nature is the greatest laboratory of all. Our future botany seems in danger of becoming myopic by reason of study being concentrated at too short focus. To correct this, young aspirants should travel early, as free lances, hazarding the fortune of the wild, as Darwin and his fellows did.

Homoplasy

I have already alluded to the tempestuous meeting of 1860 in Oxford. Shortly after it an undergraduate came up to Christ Church who, before he was of standing to take his M.A. degree, had himself made a real contribution to the philosophy of evolution. It was Ray Lankester, who in 1870 published a short paper "On the Use of the Term Homology in Modern Zoology, and the Distinction between Homogenetic and Homoplastic Agreements."[3] Its author was only twenty-three years of age, and its date barely a decade after the publication of the "Origin." This short paper went far to clear up the vague ideas surrounding the term "homology" in the minds of early evolutionists. Lankester introduced the idea of "homogeny," substituting in a more strict sense the word "homogen" for "homologue." He also sug-

[3] *Ann. and Mag. of Nat. Hist.*, vol. vi, p. 34.

gested, to avoid confusion, the use of another new term, *viz.*, "homoplasy." He defined homogeny as simply the inheritance of a common part, while homoplasy depends upon the common action of evoking causes or of a moulding environment upon homogeneous parts, *or* upon parts which for other reasons offer a likeness[1] of material to begin with.

This definition was at once adopted in the morphological study of animals, but Lankester did not himself apply it at the time to the morphology of plants. In point of fact the conception of homoplasy and the use of this clarifying term made its way but slowly into botanical literature. There is reason to believe that we are as yet only beginning to recognize in the evolution of the plastic plant-body how far-reaching has been the influence of homoplasy, not only upon external form, but also in the internal evolution of tissues. As to external form, a wide recognition of the results of homoplasy is now generally accepted for land-living plants, and in particular in respect of the origin of foliar appendages; for instance, the leaves in bryophytes and vascular plants are held as homoplastic, not as homogenetic; similarly with the leaves of bryophytes, and possibly also of pteridophytes, *inter se*. On the other hand, we may find among the larger brown algae indications of the differentiation of a supporting organ and lateral appendages from a common branch-system, that can only have been homoplastic with an origin of like parts in certain red algæ. Such conclusions, drawn from the algæ themselves as well as from the archegoniatæ, have the natural effect of raising distrust of wide comparisons between any seaweed and any land-plant in respect of foliar differentiation. Comparisons of this nature can not be held acceptable as mere guesses, by loose reference between one class and another. They would have to be based on the recognition of compact sequences within reasonably close circles of affinity before they could carry conviction.

Similarly in the morphology of the internal tissue-tracts, we are already familiar with certain examples of

homoplasy; for instance, that of secondary thickening. No one would now hold, with the school of Brongniart, that all plants with cambial activity are akin. But it is only in later years that we have come to realize the far-reaching results of homoplasy in the region of primary vascular morphology. Medullation, solenostely, polycycly and dictyostely have all arisen in more than one phyletic sequence, while the fluted form of the stele, or of the xylem-tract that it contains (which gives a stellate transverse section), is now recognized as a conformation meeting the demands that follow from increasing size, rather than as an indication of community of racial origin. These are examples of the effect of internal homoplasy. We are only now beginning to realize how far-reaching have been its results in plants as we see them. On the other hand, such realization when well assured can not fail to react upon our estimates of affinity of the organisms in which homoplasy appears. It may be going too far to trace all such results as consequences of the meeting of 1860; but the initiative was certainly given by Lankester in the years that followed.

1894

Passing from the stormy period of 1860, when the whole outlook of biological science was being transformed by the advent of evolution, to 1894, we see that the atmosphere had cleared. One result was that the evidence of descent tended to become too definite in the minds of some enthusiasts, and there was even a disposition to argue deductively from the accepted position, a tendency that is much too prevalent to-day. I feel bound to refer critically to my own contribution to that meeting, which was the statement of a theory of the strobilus. Thirty years have materially extended the field of established fact. Though certain parts of that theory relating to sterilization may still hold, in view of new and material facts, any close comparison between a vasculer strobilus as a whole and a bryophytic sporogonial head must fall.

In particular, the suggestions of progressive septation and eruption of appendicular organs can not now be upheld as accounting for the origin of a compact strobilus. The theory was stated tentatively, as a working hypothesis, and time has shown that the hypothesis does not accord with facts now known.

The outstanding feature of the Oxford meeting of 1894 was Strasburger's generalization on the periodic reduction of chromosomes. This shed a new light on the vexed question of alternation which, based on the brilliant results of Hofmeister, by this time held the field not only as an objective fact but as an evolutionary problem. The effect of Strasburger's communication was to establish the chromosome-cycle as general for plants that show sexuality. It provoked comparison with a similar cycle in animals. The recognition of both cycles took its origin in the discovery by van Beneden in 1883 that in sexual fusion the number of chromosomes is the same in both of the conjugating nuclei. Later observers have confirmed this in a multitude of instances, and disclosed the correlative reduction, or meiosis. The existence of a nuclear cycle alike in animals and in plants can not, however, be held as establishing any homogenetic unity of the two kingdoms. Comparison of the simpler forms of each indicates that the divergence of the kingdoms, if they ever had a common origin, was very early indeed, and probably antedated sexuality in either. Such similarities as they show in propagative detail, and particularly in the nuclear cycle, would be homoplastic, not homogenetic. If this be so for the two kingdoms of living things, may it not be equally true for the several phyla of plants that show sexuality; for are we not justified in assuming that sexuality arose but once in plants?

Historically this generalization of Strasburger fell like a bomb-shell into the midst of the old controversy between the rival theories of alternation, styled in the words of Celakovsky "homologous" and "antithetic." But it must be remembered that at the moment there was

no complete demonstration of a cytological alternation in any one Alga, though the facts soon followed for *Fucus* [Strasburger (1897), and Farmer and Williams (1898)]; and for *Dictyota* (Lloyd-Williams, 1897–8). We need not recite again the arguments *pro* and *con* of that old discussion. It soon lost its intensity in face of the obvious deficiency of crucial facts, which alone could lead to some final conclusion. Loose comparisons between organisms not closely allied are but the long-range artillery of morphology. Comparisons between organisms closely related are its small arms. The discussions of the nineties of last century on alternation were all engagements at long range, which could not be decisive without the use of close comparison. As the necessary facts were not then in our hands, those premature engagements might be held as drawn; and it was open to both parties still to entertain their own opinions. Meanwhile it may interest us as spectators to note the relation that exists between homoplasy as defined by Lankester in 1870, and those intimate questions that arise from Strasburger's paper to this section in 1894. The cytological facts acquired since the latter date tend to confirm the normal constancy of a nuclear cycle. Their effect has been to accentuate more than before the inconstancy of the somatic developments related to it. Like the fabulous genie let loose from its bottle, the conception of a nuclear cycle in plants that show sexuality, disclosed in 1894 by Strasburger, dominates ever more and more the morphological field.

Before discussing the relation of somatic development to that cycle, it will be well to revise the terminology. The word "homologous" has a double significance, as shown by Lankester. If it be used to include examples of "homoplasy" the whole field is open for what has been styled antithetic alternation, in which the two generations were presumed to be homoplastic. If in the sense of "homogeny," then it would be necessary to prove the relation of the somata throughout descent to the nuclear

cycle. On the other hand, the term "antithetic," while it accentuates the difference between the two somatic phases, is not explicit, in that it does not describe the method believed to have been involved in their origin. It would be well to drop these old terms, which are neither exact nor explicit, and to support a more general use of the words "*interpolation theory*" in place of "antithetic" and "*transformation theory*" in place of "homologous." These words accord better with current views and are explicit.

1926

From the time that the periodic reduction of chromosomes was recognized as general in organisms showing sexuality, the nuclear cycle has formed a natural foundation for the comparison of the life-histories of plants. The normal cycle may be figured to the mind as a closed circular thread with two knots upon it, syngamy and reduction. Between those knots beads may be strung, one, or more than one, or none. These represent somatic developments, which are normally diploid between syngamy and reduction, haploid between reduction and a fresh act of syngamy. They follow in alternate succession in any normal cycle, but either may be repeated indefinitely by vegetative propagation. Certain questions arise with regard to the evolution of these somata as we see them. The first is, how far are the diploid and haploid somata of the same cycle comparable one with another? The reply will turn upon the constancy of the events of syngamy and reduction throughout descent. If they were constant, then it appears a necessary consequence that the alternating diploid and haploid somata must have been distinct throughout their history; and any similarity which they may show, as in *Dictyota* or *Polysiphonia,* would be homoplastic. It would indeed appear natural that they should be alike in algæ, since they are parts of the same organic life, and live under identical circumstances. It has, however, been suggested that re-

duction may not be a fixed, but a movable event in the individual life: liable to be deferred or carried over to a later phase, in which case a diploid generation might arise by transformation from an already existent haploid phase. The monospores of the Nemalionales have been cited as possibly convertible in other red seaweeds into tetraspores, by some sudden deferring of the act of reduction. I am not aware that this has been advanced by close comparison beyond the position of tentative suggestion, though the existence of a diploid gametophyte and of a haploid sporophyte in certain abnormal ferns would indicate the possibility of the suggestion being true. Pending the advance of a closely reasoned argument it is best to keep an open mind.[4] Meanwhile the weight of facts hitherto known from plants at large may be held to support the stability of the events of syngamy and reduction during normal descent. The two generations of the same life-cycle would, in the absence of a carry-over of reduction, be homoplastic, not homogenetic.

It is, however, round a second question that divergent views as to alternation chiefly center. How far are the diploid and haploid somata in the cycles of different types of organism comparable one with another? This is, in fact, the old problem of Pringsheim and Celakovsky. It applies to all plants where somata alternate, but a special interest attaches to the case of land-living plants; in particular, we shall trace the origin of the dominant sporophyte of a land flora, and inquire whether it originated by *transformation* of diploid developments such as are seen in certain algæ, or by formation *de novo* through *interpolation?* A clear statement of the former hypo-

[4] Even if such a carry-over of reduction were proved to occur in certain algæ, I do not see that this would disprove interpolation in other organisms. We have been too apt to assume that all alternation arose in the same way—*either* by interpolation *or* by transformation. Among the infinite possibilities of organic nature I see little justification for assuming this. The evolutionary problem has been to impose the amplification of a vegetative system upon a nuclear cycle. I see no reason to exclude its solution in a multiplicity of ways. (*Cf.* J. Buder, "Zur Frage des Generationswechsels im Pflanzenreiche," *Ber. a. d. Bot. Gesellsch.*, 1916, p. 559.)

thetical alternative was made by Scott in 1911, *viz.*, "that the fern with its stem and leaves corresponds to the seaweed in which stem and leaf are not differentiated, the whole plant being a thallus." "On this theory the sexual prothallus and the asexual plant are both alike derived from a thallus, and may once have been perfectly similar to each other." In alluding to leafy liverworts and some of the higher seaweeds as illustrations, he then remarked that "these are only analogies, it is true." But after reference to the fossil evidence, as it then was, he concluded that it is more probable that the higher cryptogams came direct from plants of the nature of algæ than from bryophyta or any plants at all like them; he added, however, that "this view is pure hypothesis." It must, of course, be remembered that these quotations from Dr. Scott's "Evolution of Plants" (p. 225) were of pre-Rhynie date. A luminous statement of his later views was contained in his address to Section K in Edinburgh in 1921, which will be in the memory of you all.

Church, in his vivacious essay on "Thalassiophyta" (1919), went much further than this guarded and scientific statement by Scott of 1911. By "deduction from types still existent in the sea" he assumes "algæ of the transmigration" as a bridge between the vegetation of land and sea. His transmigrant algæ "appear, in fact, to have been more highly organized than any single algal type at present known to exist in the sea," and "to have combined the best features, as factors of the highest grade of progression, of the known great conventional series of marine phytobenthon, and yet to have belonged to none of them." He boldly fills the gap that puzzles us all by hypothetical organisms that no one has seen, and which he expressly tells us we shall never see (*l.c.*, p. 88). If the discussions of the nineties were inconclusive engagements at long range, what is this? It is certainly not that closer analysis advocated by Bateson.

An alternative to such an effort of imagination may be found in the examination of organisms that really exist,

or are known to have existed, illuminated by the conception of homoplasy, or, as it is often called, parallel-development. The comparisons should be based upon the recurrent fact of the chromosome-cycle, since this underlies the ontogeny of all plants that show sexuality. Somatic development in sexually produced organisms is seen to be in some measure independent of the successive events in the chromosome-cycle. The somata may be unicellular, existing only as potential gamete or zygote, respectively; they need not necessarily be alike in themselves, nor need they appear at the same points in the cycle. For instance, it is found that the pennate Diatoms have diploid vegetative cells, while in the centric Diatoms they are haploid, this latter state being shared by the vegetative cells of the Desmideæ and Zygnemeæ. That a soma should appear at the same point in the cycle of two or more organisms does not necessarily prove that they have had the same phyletic history. The full proof that they did can only follow from the observation of sequences of close relationship, which should indicate the successive steps to have been the same if a true homogeny exists. We are, in fact, thrown back upon close comparative observation for tracing truly homogenetic sequences of somatic development, rather than upon the mere position of a given soma in the cycle, or the recognition of its diploid or haploid state. Until such evidence is available it will be best to hold it as possible that the origin of any somata compared has been homoplastic.

Some such view as this was clearly in the mind of Professor Oltmanns in 1923 (*Morph. und Biol. der Algen,* vol. iii, p. 143). Speaking with the fullest knowledge of the cytologically distinct alternation as it appears in the algæ, he says: "When we affirm that an alternation of a gametophyte and a sporophyte is seen in the more highly developed algæ, that is not the equivalent of saying that all the forms cited betray an affinity to the archegoniatæ. Just as sexuality may be held to have arisen repeatedly and independently in various groups of the lower organ-

isms, so may the various higher families have carried out independently the establishment of two generations. Where a second generation is present we may assume that it was independently interpolated, and has developed from small beginnings such as we see in *Œdogonium* or *Sphæroplea*, &c." If this be admitted for various families of the algæ, it may be contemplated the more readily for the archegoniatæ, which are more distinct in their characters from the algæ than these are among themselves.

No one has yet made out a closely reasoned case for the descent of the archegoniatæ from the green, the brown or the red algæ. The old view that they originated from the green algæ has never recovered from the blow delivered by Dr. Allen, when he showed that the reduction in *Coleochæte* takes place in the first divisions of the zygote, and that the presumed primitive sporophyte is really haploid, and not cytologically a sporophyte at all. It is a perfectly tenable position to hold that the archegoniatæ sprang directly from none of these groups, as we know them. In the absence of definite comparative evidence the field appears to be open to an origin of alternation in the archegoniatæ by interpolation of a sporophyte *de novo*, developed not in water but in relation to a land-habit. Against such an origin of a sporophyte there is in some minds a strange, and to me an inexplicable, preconception. Many years ago Professor Von Goebel drew attention to a curious leaning among morphologists towards reduction-series. It appears as a prevalent psychological phenomenon that men are more prone to admit down-grade sequences than those that are up grade. But it is clear that in evolution at large there must have been a credit-balance of upward development as a whole, otherwise no multicellular organisms could exist at all. Each morphologist no doubt strikes his own financial balance at the end of the year and notes justly whether or not his credits meet his debits. Why should he not carry forward the same accurate balance of amplification against reduction into his morphology? But we find him

cheerfully accepting evidence of the practical elimination of the gametophyte in seed-plants, and contemplating a similar elimination in the brown seaweeds, thus making drafts upon his morphological account. When, however, an origin by interpolation of the sporophyte is suggested to him, he regards this morphological asset with something more than suspicion. He will overdraw his morphological balance more willingly than he will pay in assets to his morphological credit.

Here it may be well to consider what rational explanation is now possible for the origin of a diploid generation. The old biological idea that the alternation arose in relation to amphibious life will not suffice, since alternation is seen to exist in fully aquatic algæ. Nevertheless, the amphibial life may have been one of the circumstances that have modified the development, and guided it into the special channel seen in archegoniate plants. Svedelius, however, suggests a more general reason for the somatic development of a diploid sporophyte which deserves the most careful attention ("Einige Bemerkungen ueber Generationswechsel und Reduktionstheilung," 1921). Instead of laying weight upon meiosis as reconstituting the daughter-nuclei, he suggests that the greatest importance of the reduction-division lies rather in its making new combinations of chromosomes possible. He points to the difference between only one reduction in each cycle, as in the simplest organisms, and many as in those that have achieved a higher development; and he concludes that the origin of a large diploid sporophyte is thus an advantageous biological organization, since it secures many reduction-divisions, and consequently numerous new combinations. This hypothesis has the advantage of giving a general explanation of the origin of a diploid sporophyte, independently of any special circumstances of life under which it came into being.

Devonian Fossils and a Land Flora

We may here leave aside any detailed study of alternation in the thallophytes, though it is full of interest, and

the investigation of it rich in promise; particularly that of the brown seaweeds, as last year's proceedings of the section have shown. This year we may concentrate on the land flora, and inquire how recent discoveries may have affected our outlook on it. Notwithstanding that the years since 1894 have been marked by discoveries of the first rank, I see no reason to alter my belief in an interpolated sporophyte in the archegoniatæ, except in respect of the primary causality; nor do I relinquish the view that the two generations are homoplastic and not homogenetic. Indeed, the new evidence appears to me to strengthen rather than to oppose the position previously stated. I see no need materially to modify the biological reasoning which I offered in 1890 in explanation of the formal difference in land-plants between the alternating generations, nor the recognition of the stabilizing influence of the amphibious life upon them. But the new discoveries have altered the aspect in certain particulars, and in nothing more than in the relations of the bryophyta to the rest.

The most impressive event of recent times in the sphere of morphology has certainly been the recognition and constitution of a new class of vascular plants. The disclosure of the fossils of the Rhynie Chert, of early Devonian age, is not only notable as introducing in unusual detail a type of vegetation barely hinted at before, but also because those early land-plants present material of the highest importance for comparison. The new class of the Psilophytales was founded to receive them together with the old Devonian fossil *Psilophyton,* and some others; while their relation to the living Psilotaceæ is recognized. These rootless plants together present a new facet upon the problem as to the origin of members in vascular plants, though they do not wholly resolve it. Apart, however, from such conclusions as the new facts may suggest, they introduce a tonic effect into morphology. Something positive is actually seen, and of very early existence, as a set-off against reasoning from

data so often isolated and insufficient, or even purely imaginary. For a balanced statement on land-vegetation viewed in the light of the newly acquired facts one can not do better than refer to Chapter VI of Dr. Scott's book on "Extinct Plants and Problems of Evolution," 1924. Discussing the relation of the Bryophytes to other archegoniatæ, he remarks how Kidston and Lang had pointed out that the three phyla, pteridophyta, bryophyta and algæ, are undoubtedly brought nearer together by the Rhynie discoveries; and I may be pardoned for requoting from him a passage of my own (*l.c.,* p. 205): "Long ago it was remarked that the widest gap in the sequence of plants was that between the Bryophytes and the Pteridophytes. It is within this gap that the newly discovered fossils take their natural place, acting as synthetic links, and drawing together more closely the whole sequence of land-living, sporangium-bearing plants." Under the influence of these and other late discoveries the bryophyta are coming into their own. Not only has the problematical *Sporogonites* been described by Halle from the Devonian rocks, but undoubtedly liverworts of the Carboniferous Period have been disclosed by the refined methods of Walton. These events coincide with the advent of the Psilophytales, the most sporogonium-like of all vascular sporophytes. It seems there may be a natural place for *Anthoceros* at last, as Campbell tells us.

The effect of the establishment of the Rhyniaceous type on the comparison of the parts of the sporophyte is important; in particular the question of the origin of the root and leaf may be canvassed afresh. We see a class of early rootless, land-living sporophytes, sharing this feature with the Psilotales, and we may reasonably hold them to represent a primitive type. On the other hand, we see in all pteridophyte embryos which have a suspensor that the root, often late in appearance, is a lateral appendage on the embryonic spindle. Moreover, the root arises as an exogenous growth in *Phylloglossum,* and in certain species of *Lycopodium,* as do also the enigmatical

rhizophores of *Selaginella*. Provisionally, then, we may conclude that the root is a late addition to the plant-body in descent, and that it was in the first instance some form of exogenous branch at the base of the primitive sporophyte, such as is seen in the Psilotaceæ and in *Asteroxylon*.

Much greater interest and more consecutive reasoning centers on the question of the foliar developments of vascular sporophytes. Studies on "Leaf-Architecture" and passages dealing with that subject in my book on Ferns, Vol. I, have shown that by inductive comparison based on an analysis of plants now living, we may arrive at a theoretical origin of leaves of the fern-type from a dichotomously branching system; and already in 1884, long before the discovery of the Psilophytales, this conception had been tentatively extended to include the axis as well, though the material facts such as we now possess were not then in evidence. It was also concluded from comparison of living plants that the sporangia were originally distal on the branches. Thus the Psilophytales supplied in actual fact a sub-aerial type already contemplated as a result of inductive argument. If this origin of a fern-shoot by sympodial development from a dichotomous branch system, such as that of the Rhynie fossils, be true, there would be no need to draw upon supposititious "Algæ of the transmigration" to explain the origin of leaves of the fern-type, for sub-aerial plants would be seen to have originated such leaves for themselves. Any similarities between algæ and ferns in respect of foliar appendages would appear only as interesting facts of homoplasy.

This does not, however, exhaust the question of foliar origin. Such plants as *Thursophyton* and *Asteroxylon,* as well as the living Psilotaceæ, present features which suggest a second type of foliar appendage. Lignier has long ago designated these as "phylloides," while his "cauloides" correspond to the leaves of ferns. I do not propose here to discuss this difficult question. The pres-

ent purpose is fully served by showing that induction from the facts of land-living plants alone will now give a reasonable history of the origin of leaves of the Filicinean type, without any need to refer to some transmigrant alga to explain it. Why should we assume any limit to the capacity of organic nature to originate new members? Or to do this in more than one way, and in more than one phyletic line? At the back of the theory of transmigration is the assumption that she can not, or probably would not, do this. But a wide comparison of things now living before our eyes, or that have lived, shows that she can and that she has done it repeatedly.

Paleobotanical discovery has been greatly advanced within the period under review. The features of the vegetation of Mesozoic time are becoming clearer than ever before under the hands of Professor Seward. The Carboniferous Flora has been richly presented to us by Williamson, Scott, Oliver and Kidston in Britain, and by continental workers such as Renault, Zeiller, Bertrand, Nathorst and Solms-Laubach. We are now able to substitute something positive in place of vague surmisings. Not only do the new facts illuminate our knowledge of plants now living, but they also apply a check upon theories as to their origin. Latterly a vision is becoming ever more and more real of a Devonian flora, revealed by Kidston and Lang at home, and by other workers in Scandinavia, in Germany and in America. Given more extended collecting, an improving technique and the fortune of finding more material as well preserved as that at Rhynie, who knows but what the coming decades may see the land of the Devonian period clothed before our eyes by a flora no less stimulating and even more suggestive than that of the coal? But though Devonian lands are the earliest yet known to have supported a sub-aerial flora, the highly advanced structure of such a fossil as *Palæopitys Milleri* suggests that we are still far from visualizing the actual beginnings of land vegetation. Moreover, the mixture in the Rhynie Chert of algal types

with vascular land-plants presents at the moment a problem as perplexing as it is ecologically strange. It is always difficult to estimate justly the times in which we live; but we may well believe that the future historian of botany will note the present period as one specially marked by successful study of the floras of past ages and by the increasing cogency of their comparison with the vegetation of the present day.

The "Annals of Botany" as a Historical Document

Perhaps too much of your time has been claimed for morphological questions, which are closely related to the dates of the three meetings of the association here in Oxford. The brief space that remains may be devoted to a more general survey of the period which these dates cover. In this we could not do better than to take as an index the pages of the "Annals of Botany," for the existence of which we owe a deep debt to the Oxford Press. In 1860 there was no organized laboratory teaching of botany in any university in Britain; and as yet there was no journal of the nature of the "Annals." But the revival of close observational study in botany under Huxley and Thiselton Dyer at South Kensington in the early seventies, recorded last year by various writers in the "New Phytologist," was beginning to take effect in 1881, when the British Association met in York. There the outstanding feature was the address of Hooker on geographical distribution. This and the papers by Bayley Balfour on Socotra and by Baker on Madagascar were all that really mattered botanically, and almost all the contributions were systematic or regional in subject. The revival of the laboratories had not yet fructified. At this time all the work that was done in laboratories was called "physiology," as distinct from systematic botany, which was conducted on dry specimens in the herbarium. In 1887, six years after the York meeting, the *Annals of Botany* was founded through the activity of Sir Isaac Bayley Balfour, and a small committee of guarantors

whose personal security induced the Clarendon Press to make the venture. From the start that journal has paid its way. The forty stately volumes form a record, between the pages of which you may read the history of botanical progress in Britain, and in some degree also in the United States, for American botanists have always been with us in its pages. In the first issues of the *Annals,* morphology and systematic botany preponderated, and from the proceedings of the meeting of the association in Oxford in 1894 we see that this was still so. That meeting witnessed a crisis in the affairs of botany in Britain. A newly established Section I of Physiology assumed that the functional activities of plants would be swept, together with those of animals, into its hands. Up to this time Section D had been the undivided section of biology. An irregular cleavage of interests was set up by this claim, for the zoologists were mostly willing to give up their physiology, but the botanists were not. Their refusal to accept divorce of form from function contributed to, or at least coincided with, the foundation of a separate Section K of Botany, and has dictated the policy of British botany ever since.

As we pass from 1894 to the current period we perceive a marked shifting of the interest of botanists from the study of form to that of the intimate constitution and functional activity of plants. Whole fields of colloidal chemistry and physics, of quantitative physiology, of cytology and genetics, of ecology, of fungology and bacteriology have been opened up. The present century has been specially marked by the extension of opportunities for physiological research, by better equipment of departments in the universities, and by the foundation of independent establishments carrying on experimental inquiry in its broadest application. This is rapidly bringing the science into closer relation with imperial and social aims. It is needless to specify, but the effect of it all is plainly written in the pages of the *Annals.* Experimental results have gradually taken the preponder-

ant place over description and comparison, as is amply shown in the last January number. "For better, for worse," the pendulum has definitely swung over from the extreme systematic position of half a century ago, through a phase of prevalent morphology (or perhaps we should better say of organography), to an extreme physiological position at the present time. Some of you may even have felt that this address is in itself an anachronism, in that it has not touched upon the moving physiological questions of the day. While I may claim none the less to sympathize with physiological aspirations, I do not assent to any ultra-physiological aspect of botany that would degrade or minimize the comparative study of form. *"Medio tutissimus ibis"* is still a true maxim. The laboratory physiologist, dealing with the things of the moment, can not safely detach himself from the things of the past as recorded in heritable form. He should not allow himself to be immersed in statistics and neglect history. The pendulum has gone full swing, within a period of about half a century; but we may confidently anticipate a return towards some middle position.

DISCUSSION AND SHORTER ARTICLES

PHOTIC ORIENTATION IN INSECTS

In an extensive study of the process of orientation to light in the drone fly, Eristalis, and the robber fly, Proctacanthus ('23 and '24), I attempted to set forth in some detail the essential views, concerning the process of orientation in organisms, held by Verworn, Loeb, Bohn, Garrey and others. In this attempt I reached the conclusion ('23, p. 111) that these authors maintain that orientation is the result of a balance between the effect of the rate or extent of movement of the locomotor appendages on opposite sides, just as it is in a row boat which has no rudder and is propelled and guided with oars, that the rate of movement in the appendages is directly proportional to the amount of light received by the receptors connected with them, that the processes involved are not dependent upon the location of the stimulus in the receptors, that the stimulating agent acts continuously, not intermittently, and that the orientating stimulus continues after the organism is oriented just as it does during the process of orientation.

There appears to be serious misunderstanding on the part of some investigators as to the meaning I attach to the phrase "rate or extent of movement of the locomotor appendages on opposite sides." Referring to this, Crozier and Federighi ('24a, p. 157) say: "With arthropods the tension of locomotor muscles on the one hand, and on the other the matter of the rapidity of their phasic contractions, have sometimes been preposterously confused" (Mast, 1923–24); and ('24b, p. 217): "The respective rôles of the rapidity of leg movements and of the postures of the legs during the course of orientation by light have, however, never been made clear. The fact that an experienced observer (*e.g.*, Mast, 1923–24) can at this late date make an inexcusable confusion between tonic effects determining limb posture and the frequency of leg movements shows that the point here raised is especially worth settling by means of a crucial test."

These two authors evidently hold that in the phrase in question I assert that Verworn, Loeb, Bohn, Garrey and others maintain that in the process of orientation the number of steps or strokes per unit time is greater on one side than it is on the other and they devote an entire paper ('24b) to the demolition of this

idea, this "inexcusable," "preposterous" idea. They conclude (p. 220): "The notion that orientation is due to a relatively greater frequency of leg movements on one side of the body is definitely disposed of." However, no one, as far as I am aware, ever held such a notion. Why then devote so much time and so much space to its destruction?

Crozier and Federighi apparently assume that the phrase "rate or extent of movement of the appendages" necessarily refers to the number of discrete movements per unit time. It is, however, perfectly plain that it may also refer to the distance travelled per unit time. It is in this latter sense that I used the phrase, and it seems to me that, while this is not specifically stated in my papers, there are a number of references which should make it evident. For example, I say (p. 110): "In an insect which is not oriented the legs on one side, according to this view [the view of Verworn, Bohn, Loeb, Garrey and others], take longer steps and consequently move faster than those on the opposite side, causing it to turn just as a boat turns when the oars on one side move faster and more efficiently than those on the the other"; and (p. 114): "The turning toward the light is . . . due to a difference in the rate of locomotion, a difference in the size of the steps on opposite sides." In view of these and various other similar statements, and the fact that I nowhere use the phrase "frequency of movements," I am at a loss to know how Crozier and Federighi (p. 220) came to the conclusion that I assert that it is held that "orientation is due to a relatively greater frequency of leg movements on one side of the body than on the other." This is especially difficult to comprehend, since these authors in a figure illustrating the process of orientation in Ranatra ('24a) represent the steps on one side more than three times as long as on the other, indicating clearly that while the number of steps per unit time is the same on opposite sides, the feet on one side travel faster, *i.e.*, a greater distance in the same time, than those on the other.

These authors assert ('24b, p. 220) that: "Definite proof is obtained that in the phototropic orientation[1] of Ranatra the rela-

[1] It seems to me that "phototropic orientation" is an unhappy combination. Tropic, from the Greek τροπικός, means literally pertaining to a turn or a change, or the process of turning or changing. The process of orientation consists of turning. "Phototropic orientation" would then mean photo-orienting orientation or some such tautological combination. It would consequently seem expedient to use photic orientation in place of "phototropic orientation."

tive postures of the appendages, resulting in a bilateral difference of the effective stroke in swimming, is the mechanism of orientation." The proof of the adequacy of the explanation presented is, I think, essentially the same as that offered by a number of earlier investigators. I have rejected this explanation because, while it may be in accord with the process of turning under the conditions studied by Crozier and Federighi, namely, turning in specimens of Ranatra with only one functional eye, it fails in other insects to account for orientation under these conditions and under a considerable number of other conditions, especially the following (Mast, '24, p. 275):

1. "Orientation in specimens with some of the legs on one side removed."
2. "Turning upward or downward while the two eyes are continuously equally illuminated. This is evident in insects on the wing when they turn upward or downward toward a source of light."
3. "Turning in one direction while leaning in the opposite direction." "This occurs frequently in specimens with the upper portion of one eye and the lower portion of the other covered."
4. Orientation in normal specimens when it occurs without any perceptible difference in the flexure of the legs on opposite sides as has often been observed.

In none of these is there any indication that orientation is due to "*the relative posture of the appendages* on opposite sides resulting in a bilateral difference in the effective stroke." The facts that insects with legs on one side removed still orient, and that on the wing they turn, under certain conditions, directly toward the dorsal or the ventral surface in orienting seem to prove conclusively that orientation in these forms is not necessarily dependent upon anything in the nature of a difference of any kind in the action of the legs or wings on opposite sides.

I have been able to account for all of the facts in hand only on the assumption that orientation in insects is the result of a series of reflexes specifically related to the location of the stimuli in the eyes, as well as to the intensity, the time rate of change in the intensity and the size of the area stimulated, a given stimulus located in the anterior region of one eye, *e.g.*, resulting in a very different series of reflexes from the same stimulus located in the

posterior regions of the same eye, and in a still different series if there is simultaneously another stimulus in the other eye or elsewhere in the same eye. Further details regarding these views have been presented in the publications cited above.

It is, of course, a simple matter to give a much less complicated explanation if some or all of the facts referred to above are ignored, as has been done by a number of investigators. But what value can there be in a theory that is at best in accord with only a very limited number of the processes which it is supposed to elucidate, *e.g.*, a theory of orientation that is not in accord with any of the fundamental processes mentioned above? Theories of this sort are, in my opinion, pernicious; not merely because they are deceptive, but also because, owing to their simplicity and their apparent plausibility, they discourage rather than encourage further investigation.

S. O. Mast

The Johns Hopkins University

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HYBRID VIGOR AND TUMORS IN MICE

The hybrid between Japanese waltzing and a strain of the common house-mouse type has been found to be more susceptible to implanted tumor than the waltzing parent, while the other parental type is immune. Arguing from this Castle[1] is inclined to favor the older interpretation of hybrid vigor as being due to a physiological stimulus arising from the interaction of different genetic factors as opposed to the more recent conception of the accumulation of dominant favorable growth factors. This particular case in mice gives evidence of hybrid vigor in increased fertility, faster rate of growth and greater longevity. Other cases in which immunity is lacking in the first generation are

[1] Castle, W. E., 1926, "The Explanation of Hybrid Vigor," Proc. Nat. Acad. Sc. 12.

[2] Biffen, R. H., 1905, "Mendel's Laws of Inheritance and Wheat Breeding," *Jour. Agri. Sci.*, Cambridge, 1.

known. Biffen[2] reported a hybrid between varieties of wheat that differed in severity of rust infection which was as susceptible as the injured parental type.

The dominance hypothesis of hybrid vigor has never assumed that all factors favorable to growth and reproduction were completely expressed in the hybrid offspring, but only that many of them were at least partially so. The majority of cases in which this is true must certainly be carefully considered.

Take a very simple and striking illustration from maize, whereby two hereditary dwarf forms, neither of which grows over two or three feet in height, when crossed give a first generation progeny growing from seven to eight feet tall and many times more productive than either parent. Crosses between the most diverse kinds of maize known will not give as great an increase in size and reproductive ability as this cross between two types which do not differ greatly except in two factors determining height. It is quite obvious that the increased size of the hybrid in this cross is primarily due to the two dominant factors, one contributed by each parent. One could multiply such cases many times where the principal hereditary factors involved are known.

In the same way we can reasonably suppose, in spite of Castle's affirmation to the contrary, that many of the favorable growth factors from the house mouse combined with other factors having a similar effect from the Japanese type give the hybrid its increased vigor. The fact that in this case dominance is not complete for all favorable characters, that the hybrid is susceptible to tumor, is unfortunate for the mouse but does not necessarily destroy the usefulness of this interpretation.

Hybrid vigor acts in much the same way as a favorable environment. There are instances in which the severity of disease infection, at least in plants, is increased under favorable growing conditions. It may be that tumor in mice acts in the same way. The greater growth of the hybrid along with the increased cell activity, as Castle suggests, may favor the development of tumor, irrespective of how the hybrid vigor is brought about.

Critical evidence upon which one can decide the value of these two hypotheses, attempting to account for hybrid vigor, is found in the attainment of homozygous individuals derived from a cross-bred race which are as vigorous as the original stock. These have been obtained in rats by King[3] and in cucurbits by Cum-

[3] King, H. D., 1918, "Studies on Inbreeding, I–III," *Jour. Exp. Zool.*, 26.

mings and Stone.[4] How can these be accounted for on the assumption of an added stimulus from heterozygosity? On the dominance hypothesis segregation has brought many of the favorable factors into a homozygous combination and these factors are just as effective or more so in that condition as when heterozygous.

Furthermore, the assumption of a stimulus from heterozygosity has carried the implication that naturally cross-fertilized organisms are inherently more vigorous and productive than those naturally inbred and this is not supported by a comparison of maize, alfalfa, cabbage, squash—plants that are largely cross-fertilized, with wheat, rice, barley, beans, peas, tomatoes—plants that are naturally almost completely self-fertilized in every generation. The comparison is made between cultivated plants because their productiveness is known. The same situation exists in wild species.

The added statement made by Castle, that hybrid vigor is one of the chief reasons why bisexual reproduction is so wide-spread, does not agree with the generally accepted opinion that the principal advantage of this method of reproduction lies in the increased variability and consequent elasticity in adaptiveness to new and varied surroundings, but this has nothing to do with the interpretation of hybrid vigor.

D. F. Jones

Connecticut Agricultural Experiment Station

A SECOND GENE PRODUCING GOLDEN PLANT COLOR IN MAIZE

Introduction

Golden plant color in maize was first reported by Emerson[1] in 1912. He found it to be inherited as a simple Mendelian recessive to the normal green. Later investigations by Lindstrom[2,3] have shown the factor concerned in the production of

[4] Cummings, M. B., and Stone, W. C., 1921, "Yield and Quality in Hubbard Squash," Vermont A. E. S. Bull. 222.

[1] Emerson, R. A., Nebr. Agr. Exp. Sta., Ann. Rept. 25: 89–105. 1912.

[2,3] Lindstrom, E. W., "Linkage in Maize: Aleurone and Chlorophyll Factors," Amer. Nat., 51: 225–237. 1917; "Chlorophyll Inheritance in Maize," Cornell Univ. Agr. Exp. Sta. Mem. 13: 1–68. 1918.

golden plant color to be in the same linkage group as the *R* factor for aleurone color and the l_1 factor for yellow seedlings. This group has been designated by Lindstrom[4] as the second linkage group in maize. More recently a number of other genes have been found to be in this group.

The purpose of the present paper is to report the isolation of a second factor for golden plant color which is complementary to the original golden producing factor. For convenience in nomenclature the original golden producing gene reported by Emerson is designated as golden 1 (g_1) and the new factor for golden plants as golden 2 (g_2).

Golden 2 is very similar in its appearance to golden 1. In fact, in progenies segregating for both golden 1 and golden 2 it has not been possible to distinguish visually between the two types definitely. As a rule, however, plants of golden 2 are inclined to be a paler yellow green than those of golden 1. Many of the golden 2 plants also seem to have somewhat of a silvery cast to them.

Origin of g_2

During the season of 1923 2,493 individual ear rows of corn were grown in connection with the corn-breeding investigations conducted cooperatively by the Office of Cereal Crops and Diseases, U. S. Department of Agriculture, and the Farm Crops Section, Iowa Agricultural Experiment Station. These ear rows represented the first inbred generation of a number of commercial varieties of corn. Many of the rows segregated for different chlorophyll variations, and among these segregating rows were seventeen which contained golden plants.

In order to determine how many genetically distinct kinds of golden plants were present, plants from different rows were intercrossed. Plants in these rows also were crossed with plants from a strain of the original golden, seed of which was kindly supplied by Dr. E. W. Lindstrom, of the Department of Genetics, Iowa State College. Some of the crosses to determine the number of genetically distinct goldens present were made in 1923 and the remainder in 1924.

The progenies grown from these crosses showed that the golden plants in some of the rows were genetically identical with the

[4] Lindstrom, E. W., "Genetical Research with Maize," *Genetica* 5: 327–356. 1923.

original golden 1, but that a new golden producing factor, golden 2, also was present. Table 1 shows the pedigrees of the seventeen segregating rows, the varieties from which the seed came and the golden factor which was determined to be present.

TABLE 1

Rows from Selfed Ears of Corn that Segregated for Golden Plants, the Varieties from Which the Seed Came, and the Golden Producing Gene Found to be Present

Pedigree Number	Variety	Golden
202–1	Iodent	g_2
–2	"	g_2
–5	"	g_2
230–5	"	g_2
234–3	"	g_2
250–4	"	g_2
259–1	"	g_2
–5	"	g_2
262–2	"	g_2
270–3	"	g_2
285–3	Doctor Yellow Dent	g_1
–5	" " "	g_1
351–1	Black's Reid Yellow Dent	g_2
–3	" " " "	g_2
483–2	Argentine Flint	g_1
–4	" "	g_1
487–4	" "	g_1

As shown in Table 1, golden 1 was isolated from Doctor Yellow Dent and from Argentine Flint in the experiments herein reported. It was found first by Emerson in a plat of silage corn grown at Lincoln, Nebraska, in 1910. These are widely different varieties with little chance of any immediate common parentage. Golden 2 appeared in Iodent, the Iowa Station selection of Reid Yellow Dent and in Black's strain of Reid Yellow Dent. Since these are both selections from Reid Yellow Dent there is a chance of common parentage here.

Defective characters due to the same genetic factor and found in widely different varieties of maize are of special interest. They may have arisen by mutation comparatively early in the development of the species and been maintained by the absence

of effective selection due to the hetrozygous condition of maize. On the other hand, such defects may be determined by genes which mutate with more or less frequency.

Inheritance

Golden 2, like golden 1, has been found to behave as a simple Mendelian recessive. Data from forty-four segregating rows have shown 1,323 green plants and 373 golden plants to occur where 1,272 green plants and 424 golden plants were expected from theory. This is a difference of 51 ± 33.6. Eight back-cross progenies had a total of 140 green and 156 golden plants, where the theoretically expected numbers were 148 greens and 148 goldens. In this case $\frac{\text{Dev.}}{\text{P.E.}} = .43$. Counts on forty-eight progenies grown from seed from self-pollinated green plants in segregating rows showed sixteen to be homozygous green and thirty-two to be segregating, exactly the numbers expected from theory.

A number of crosses have been made between golden 1 and golden 2. The F_1 of this cross has been green in every case. The F_2 progenies have given 9 : 7 ratios of greens to goldens, in-

TABLE 2

Number of Green and Golden Plants in the F_2 Progenies of the Cross $g_1\ g_1\ G_2\ G_2 \times G_1\ G_1\ g_2\ g_2$

Pedigree Number	Number of Plants of the Kind Stated Green	Golden
3286	94	58
3287	119	62
3288	103	66
3289	102	76
3290	110	54
3291	99	67
3292	84	49
3293	56	48
3294	77	55
Totals	844	535
Expected (9 : 7 ratio)	776	603
Deviation	+ 68	− 68

$\frac{\text{Dev.}}{\text{P. E.}} = 1.73.$

dicating a complementary action between the two genes. The F_2 data are given in Table 2.

It will be noticed from the F_2 data in Table 2 that there is a deficiency of golden plants. Many of the golden plants in the above F_2 progenies were extremely weak. The deficiency, therefore, may be due to the weakness of the double recessive plants, some of which may not live. The data show further that there is no evidence of linkage between golden 1 and golden 2. They came into the cross from opposite parents and any linkage would tend to produce an excess of golden plants rather than a deficiency.

SUMMARY

A second factor influencing the production of golden plant color has been isolated and found to behave as a simple Mendelian recessive.

For convenience in nomenclature the original golden producing factor has been designated as golden 1 (g_1) and the new factor as golden 2 (g_2).

The factor pairs for golden 1 and golden 2 have been found to exhibit a complementary action toward one another.

G_1g_1 and G_2g_2 do not appear to be linked.

MERLE T. JENKINS

BUREAU OF PLANT INDUSTRY,
U. S. DEPARTMENT OF AGRICULTURE

MENDELIAN INHERITANCE IN HYBRID WARBLERS

In connection with the short article under this heading which appeared in the July–August number of the AMERICAN NATURALIST may I be permitted to point out that a Mendelian interpretation of the phenomenon of hybridity in these warblers was put forward some years ago by Bateson? It is to be found on pp. 157–158 of his "Problems of Genetics" published by the Yale University Press in 1913. The suggestions there put forward are essentially similar to those which Mr. Morss, apparently in ignorance of what Bateson wrote, has recently advanced in this journal. The chief point of difference is that Bateson assumed the character of black throat and auriculars found in *V. chrysoptera* to be dominant to the condition in *V. pinus* in which these markings are not present. Mr. Morss however assumes the black markings to be recessive, and his analysis of the data collected from Chapman's "Warblers of North America" seems to indicate that on this point he is probably correct.

R. C. PUNNETT